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STUDIES ON THE EARTHWORM FAUNA OF PENNINE MOORLAND

by

JOHN ALAN SVENDSEN

- being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1955.

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STUDIES ON THE EARTHWORM FAUNA OF PENNINE MOORLAND.

Introduction and Historical Review.

The Lumbricidae are a relatively modern, successful family of the phylum Annelida and of the approximately two hundred and twenty species, nineteen are peregrine and the remainder endemic. Of the British fauna, seventeen of the peregrine forms are included in the total of twenty-seven species and ten varieties. (Cernosvitov and Evans, 1947)

The term 'earthworm' is generally restricted to this family in Gt. Britain since its representatives are the only soil living Oligochaetes large enough to claim public attention. In other English speaking countries the word is not so constrained and may be applied to members of various families, e.g., the 'oriental earthworm', Pheretima hupeinsis. (Schread, 1952) In spite of this ambiguity 'earthworm' is such a well known term that it is difficult to avoid its use without a feeling of pretension. Nevertheless, with the exception of the title, the expression is avoided throughout this work.

Recognition of species in the Lumbricidae is made difficult by the small number of systematic characters available. Although many problems still exist, Cernosvitov (1942) cleared up the confusion over the British fauna left by Friend (1891-1928). Muldal (1952a) confirmed, by chromosome counts, the validity of most species occurring in Britain. At the same time both he and earlier, Pop (1941) suggested that there should be some revision in the generic classification. The Linnean society Key to the Lumbricidae (Cernosvitov and Evans, 1947) follows the division of the family into eight genera after, Svetlov (1924) Cognetti (1927) Michaelson (1928) and Stephenson (1930). This system is still in common use and is the one followed in this work.

Darwin (1881) showed by observation and experiment that 'the earthworm' had a variety of habits and he discussed their effects on their environment. He did not, however, distinguish species and it seems probable that his observations cover several, rather than the one assumed.

Later work falls into two categories, the ecological and the experimental.

The experimental workers tended to ignore the variety of the Lumbricidae and generally used only one species for their studies. Stephenson (1930) in reference to these workers says:-

"I cannot banish from my mind the idea that a number of workers who scarcely appreciate either the large number of genera and species or the great variety of structure which they present, consider any earthworm of fair size that they find suitable for their work to be 'the common earthworm, _Lumbricus terrestris_'.

In working on the influence of light, Parker and Arkin (1901) and Smith (1902) used _Eisenia foetida_ while Walton (1927) and Hess (1924 and 1925) used _Lumbricus terrestris_. On the effects of salts, Parker and Metcalf (1906) used _Eisenia foetida_ and of acids, alkalis or pH Shohl (1914) and Hurwitz (1910) used _Eisenia foetida_; Crozier (1918) used '_Allolobophora spp._'; Moore (1922) does not distinguish species; Arrhenius (1921) used _Perichaeta indica_ (Fam. Megascolecidae) and Steagall (1925) compared _Octolasium lacteum_, _Eisenia_ foetida, Lumbricus terrestris and a Megascolecid. In other reactions Parker and Parshley (1911), Yerkes (1912) and Smith (1902) used _Eisenia foetida_; Bittner et. als (1915) used 'Allolobophora spp.' and Wolf (1938), Jennings (1906) and Mangold (1951) used _Lumbricus terrestris_. Robertson (1936) in discussing the function of the calciferous glands compared _Lumbricus terrestris_, _Eisenia foetida_ and _Allolobophora caliginosa_. In investigating anaerobic metabolism Davis and Slater (1928) used _Lumbricus terrestris_ and in discussing the importance of casts Shrikhande (1950) does not distinguish species.

Much of this work is limited in value by the lack of comparisons between species and the doubts about identification. This is particularly true for the ecologist since _Lumbricus terrestris_ and _Eisenia foetida_ are rarely, if ever, the most important species in an area.

After the earlier workers tendency to lump all the species of Lumbricidae as one, 'the earthworm' (Darwin, 1881), ecologists have become increasingly aware of the importance of describing the habitat at the species level. From Müller (1889) to Guild (1952a) this has been attempted and to some extent a correlation of species with habitat has emerged, although little advance has been made since Bornebusch (1930).

Detailed work has been hampered by the difficulties of accurate identification and by poor sampling methods. Thus Kollmansperger (1934) and Pickford (1926) were unable to separate immature forms while the numbers found by different workers in apparently similar habitats range from tens per square metre, (Dreidax,1931; Evans and Guild, and Guild, 1947-1952) to hundreds per square metre, (Bornebusch, 1930; Kollmansperger, 1934 and Nielson, 1951).

The studies on the Lumbricidae of Pennine moorland, which form the subject of this thesis, were undertaken at the Nature Conservancy reserve, N.R.80, Moor House. This reserve, formerly a grouse moor, is situated in the Pennine range, south-east of Cross Fell and the source of the River Tees. It includes Great Dun, Little Dun and Knock Fells and the bulk of its 10,000 acres lie above 1,800ft. The aim of the work was to demonstrate associations between the habitats and species of the area, with especial reference to habitats which are characteristic of Pennine moorland.

Before the investigation proper, it was necessary to devize a suitable method of sampling Lumbricid populations and identifying the species found. These problems and their solutions are discussed in Part I. Part II deals with the biology of those species associated with sheep dung and Part III, the distribution of Lumbricidae at Moor House related to 'habitat'. The thesis is concluded, in Part IV, with a brief discussion of some points of general importance.

PART I

I. Systematics.

1. Species list.

Fourteen species of the Lumbricidae have been found on the Moor House reserve, N.R.80.

These are :-

Genus : Lumbricus Linné :

castaneus (Savigny)

festivus (Savigny)

rubellus Hoffmeister

terrestris L.

Genus : Allolobophora Eisen em Rosa :

caliginosa f.typica (Savigny)

chlorotica (Savigny)

terrestris f.longa (Ude)

Genus : Dendrobaena Eisen em Rosa :

octaedra (Savigny)

rubida (Savigny)

Genus : Octolasium Oerley :

cyaneum (Savigny)

lacteum (Oerley)

Genus : _Eisenia_ Malm em Michaelson :

rosea mut.macedonica (Rosa)

mut.hercynia (Michaelson)

Genus : _Eiseniella_ Michaelson :

tetraedra f.typica (Savigny)

Genus : _Bimastus_ Moore :

eiseni (Levinsen)

Type specimens of these species are deposited at the British Museum and their B.M. numbers listed in Appendix 1.

With the exception of _E.rosea mut. macedonica_, these are all species with a world wide distribution. Thus thirteen of the seventeen peregrine species of the British fauna are found at Moor House. This suggestion of the wide range of climatic conditions which the Lumbricidae can tolerate is discussed in more detail in Part II.

2. _Identification of Species_.

Mature specimens were identified with the aid of the Linnean Society key to the Lumbricidae (Cernosvitov and Evans,1947). This key contains some errors in the delineation of authorities and also in the description of the genital setae of *Allolobophora terrestris f.longa*, where 9-12 should read 9-11. It is no longer complete Muldal (1952b) (nov.sp. *Allolobophora minima* Muldal) and Davies (1954) new record: *Allolobophora arnoldii* Gates. Other new records may soon be added (per.comm.Satchell,1955) and a recently published German key by Graff (1953) changes the status of many species. Nevertheless, the Linnean Society key remains an invaluable aid to the identification of the British Lumbricidae.

There is at present no systematist working on the Lumbricidae of Great Britain,(per.comm.N.Tebble) and I have, therefore, been unable to have the Moor House species checked by an authority.

The identification of immature forms is difficult since the normally used systematic characters are sexual and therefore, undeveloped.

Five general non-sexual characters occur and these can be used as a basis for the separation of immature forms:-

1. The presence or absence of pigment. (Pop,1941)

2. The appearance of the prostomium. (Cernosvitov and Evans,1947)

3. The position of the setae.
(Pop, 1941) and
(Cernosvitov and Evans, 1947)

4. The position of the dorsal pore.
(Cernosvitov and Evans, 1947)

5. The number of segments.
(Cernosvitov and Evans, 1947
and Evans, 1946a)

The first three characters are definite and relatively easy to determine; the position of the dorsal pore may vary a little and in some cases is difficult to determine; counting the number of segments is tedious and useless in damaged specimens.

Less general characters may occur and one which is used in the following key is the swollen appearance of segments 16,17 and 18 in _E. rosea mut. macedonica_. This character is illustrated in Plate 1 p.11 which also shows the comparitive position and appearance of the dorsal pores in _E. rosea mut. macedonica_, _A. chlorotica_ and _A. caliginosa_.

Other special characters appear as a result of preservation in Formalin (4%), (Evans and Guild, 1947b). Plate 2 p.12, demonstrates the different shapes assumed by _Bimastus eiseni_ and _Dendrobaena octaedra_ during preservation. _D. octaedra_ coils while _B. eiseni_ remains relatively straight. These

PLATE 1.

White square = 1mm.

Eisenia rosea m.macedonica   Allolobophora caliginosa

Allolobophora chlorotica

PLATE 2.

Bimastus eiseni Dendrobaena octaedra

differences are useful since these two species commonly occur together but separately from the other twelve.

The character is not, however, used in the key since this is based on the assumption that any immature worm examined may belong to any of the fourteen species named. In practice this assumption may be waived when the distribution of the species (Pts.II and III) assists the weaker points in the separation.

3. Key to the Immature Specimens of the Lumbricidae of Moor House.

1.	Worms pigmented	2
	Worms unpigmented	8
2.	Prostomium tanylobous	3
	Prostomium epi or prolobous	7
3.	Hind setae closely paired	4
	Hind setae distantly paired	*Dendrobaena octaedra*
4.	1st.dorsal pore between segments 5-6	5
	1st.dorsal pore between segments 7-8-9	6
5.	'Tail' flattened, little pigment except for mid-dorsal stripe.	*Lumbricus festivus*
	'Tail' round, dark pigmented	*Bimastus eiseni*

Lumbricus rubellus Hoffmeister (Fig.1a p.18)

100 specimens examined.

Length: 2.84mm. Range: 1.60-3.54mm.

Width: 2.22mm. Range; 1.60-2.91mm.

Length/Width ratio : 1.28

Colour: Dirty olive brown (Pickled olives)

Density: Opaque

Surface texture: Matt,covered in fibrous material and foreign matter.

Poles: Both poles end in small thin spikes, one pole more pointed than the other.

Markings: None

Dendrobaena rubida (Savigny) (Fig.1b p.18)

100 specimens examined.

Length: 2.33mm. Range: 1.66-3.26mm.

Width: 1.94mm. Range: 1.54-2.34mm.

Length/Width ratio : 1.21

Colour: Varied, pale green- greenish yellow (Etiolated vegetation)

Density: Opaque

Surface texture: Smooth and clean

Poles: One ends as a firm spike, the other as a conical tuft of thin, folded material.

Markings: Latitudinal folding,more marked at the poles, sometimes overall, sometimes absent except at the tuft pole.

Dendrobaena octaedra (Savigny) (Fig.1c p.18)

100 specimens examined.

Length: 2.39mm.   Range: 1.66-3.09mm.

Width: 1.92mm.   Range: 1.60-2.23mm.

Length/Width ratio : 1.25

Colour: Off white,poles brown.   (Pickled onions)

Density: Opaque

Surface texture: Smooth, reflective.

Poles: One pole ends as a spike,the other as a stump.

Markings: Sometimes one latitudinal fold before the dark part of the stump and sometimes an internal line projects towards the centre from the stump pole.

Bimastus eiseni (Levinsen) (Fig.1d p.18)

80 specimens examined.

Length: 3.74mm.   Range: 2.86-4.86mm.

Width: 2.96mm.   Range: 2.23-3.51mm.

Length/Width ratio : 1.26

Colour: Golden brown.   (Golden syrup)

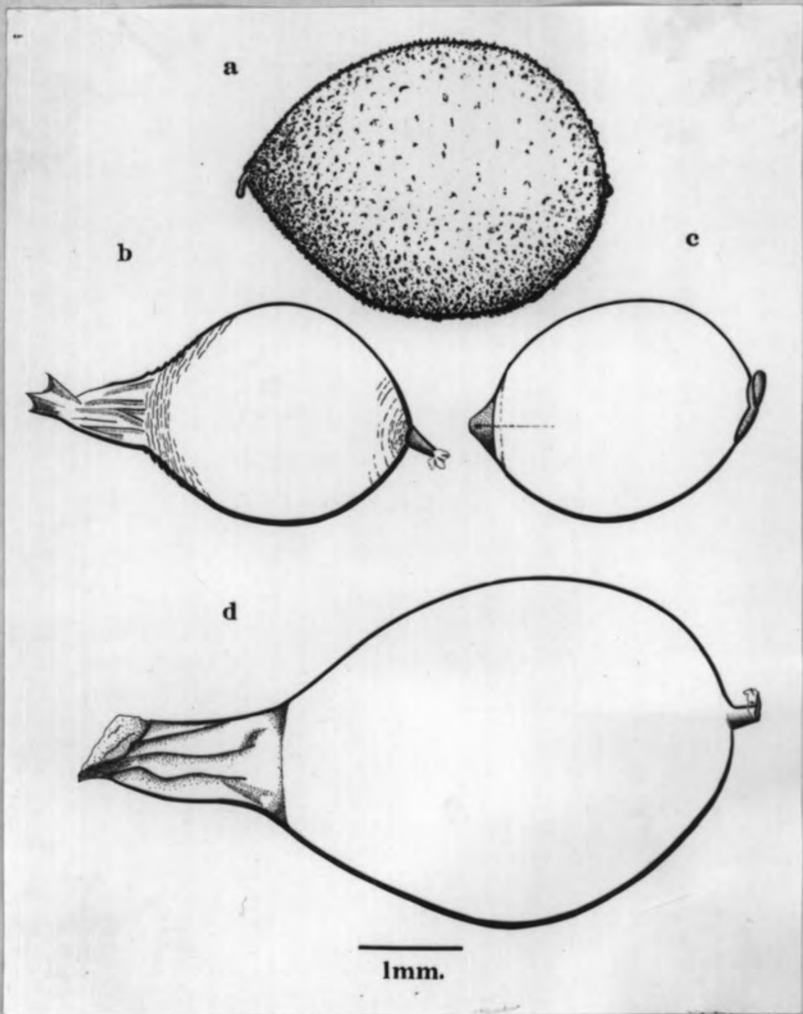
Density: Translucent.

Surface texture: Smooth and clean.Finely rugose under high power (x30)

Poles: One pole ends as a firm spike, the other as a conical tuft often flattened in one plane.

Markings: None

FIG.1.



a. Lumbricus rubellus

b. Dendrobaena rubida   c. Dendrobaena octaedra

d. Bimastus eiseni

II Population Sampling Methods.

1. Review of quantitative Population studies of the Lumbricidae.

The methods used for quantitative estimates of Lumbricid populations are summarised under three headings:-

(a) The mechanical extraction of a known amount of soil and removal of the worms by hand sorting.

(b) The saturation of an area with a chemical vermifuge and collection of the emergent worms.

(c) The passage of electric currents through an estimated volume of soil and collection of the emergent worms.

The electrical method appears to have developed from commercial gadgets used by anglers to collect bait (Walton,1933). Neither Walton nor Doekson (1950), in discussing this method, give any detailed results, they both, however, conclude that the technique is unsatisfactory for quantitative estimations.Satchell (1955a) has developed this method and claims its use gives an accurate representation of the species composition. He fails, however, to demonstrate clearly its value for quantitative estimates. The results quoted in Table 1 from Satchell (1955b) suggests that the method seriously underestimates the total population.

The employment of a chemical vermifuge was developed after the use by greenkeepers of various substances which expelled Lumbricids from lawns etc. (Evans and Guild 1947b). Evans and Guild used a solution of potassium permanganate 1.5g. per litre, at the rate of 6.8 litres per square metre. Since 1947 these authors have used this method extensively in a series of population studies, (Evans and Guild, 1947b,1948a,b and Guild, 1948,1951a,b and 1952a and b). Table 1 p.21, includes some population estimates obtained by this technique.

The extraction of a known quantity of soil and the removal of the Lumbricids by hand sorting to give a population estimate has been practised since the mid-nineteenth century, (Hensen, 1877). Some of the results obtained by a few workers from that time to the present are given below, Table 1 p.21.

In this table all the estimates are given as numbers per square metre, although the areas given in the original work vary.

TABLE 1

Author		Habitat	No. per sq.m.
Hensen	1877	Garden Soil	13.3
Müller	1878	Beech Mull	100's
Pickford	1926	Ditch, Wicken Fen	818.1
Pickford	1926	Juncus roots	96.9
Bornebusch	1930	Danish Oak Mull	358.0
Bornebusch	1930	Spruce raw Humus	18.0
Dreidax	1931	Deciduous Woodland	32.5
Kollmansperger	1934	Pasture	390.0
Drift	1951	Raw leaf litter	30.0
Nielson	1951	N.Z. pasture (1 sp.)	861.1
*Evans and Guild	1948b	Pasture	113.4
*Guild	1948	Peaty acid soil	12.4
+Satchell	1955b	Pasture 1951	166.1
+Satchell	1955b	Pasture 1952	81.94

* Estimates obtained with the permanganate technique

\+ Estimates obtained with the electrical technique

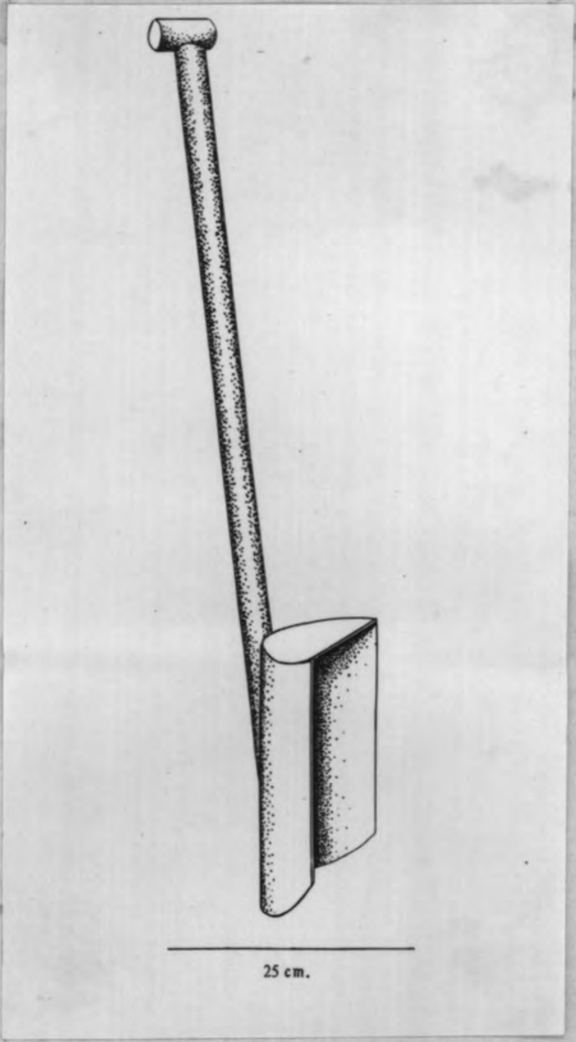
2. <u>Sampling method used throughout the present study</u>.

It was decided to use a mechanical method of sampling and at first a spade was employed to dig 20cm. cubes which were then hand sorted. Although the spade blade was flattened to allow greater accuracy, errors of up to 10% were common in the surface area of samples cut. A circular sampler was devised to overcome this error.

Basically this is a half cylinder with one end open which is sharpened to act as a cutting edge and the other closed to give mechanical strength. The diameter of the sampler is 19cm., thus, it cuts a core with a surface area of 284cm. so that 35 are needed to complete a square metre. In use the sampler is pushed vertically into the ground three times, the second and third cuts being guided by their predecessor. The soil cores are accurate in surface area but may still vary in depth due to breakage on extraction. When this occurs the hole is cleared by hand to the required depth. The maximum practical depth to which cores can be cut by this sampler is 20cm..

The instrument is illustrated in Fig.2 p.23.

FIG.2.



3. An experimental comparison of the permanganate and soil sampling methods.

Introduction.

A test of the efficacy of the permanganate method (Evans and Guild,1947b) against that of the soil sampler described above was made in September 1954. The site selected for the experiment was an apparently homogeneous area of permanent pasture at the Durham County Council School of Agriculture, Houghall Farm. The soil is light in nature and of alluvial origin which should have allowed rapid penetration of the permanganate solution. September was chosen as a time of year when the Lumbricidae are active since the permanganate technique is said to be at its most effective under those conditions, (Guild,1951a). The experiment was spread over five days; from 7th.-11th. of September 1954.

Method

In each of ten loci, chosen at random over the site, a permanganate sample of 1 square metre was taken and the treatment repeated after an interval of two hours. Five soil cores were removed from the adjacent but unaffected area of each permanganate sample. Thus, a 1 square metre permanganate sample was compared ten times with 1/7th. of a square metre of soil cores. The second treatment was given to determine what proportion of the susceptible population was affected by the first permanganate treatment.

As a guide to the remaining population, one soil core was taken from the centre of each of the ten permanganate sample areas immediately after the second treatment.

Results.

The number of worms per locus found by; the 1st. permanganate treatment (1 square metre); the 2nd. permanganate treatment (1 square metre); the soil cores from the unaffected area (1/7th.of a square metre) and the soil cores following the permanganate treatments (1/35th.of a square metre) are given in Table 2 p.26.

Six species were found on the site:-

TABLE 2

TOTALS PER LOCUS

Locus	Soil Cores	1st.p. treat.	2nd.p. treat.	Soil Cores after p. treatments
1	55	36	16	9.5
2	88.5	21	31	7
3	61.5	57	48	8
4	71.5	26	24	4.5
5	61	28	25	8
6	57.5	29	21	9
7	54	36	20	4
8	64	46	44	9
9	69	37	33	7
10	57.5	34	32	14.5
Total	639.5	350	294	80.5

Genus : *Lumbricus* Linne :

castaneus (Savigny)

terrestris L.

Genus : *Allolobophora* Eisen em Rosa :

caliginosa f.typica (Savigny)

terrestris f.longa (Ude)

Genus : *Octolasium* Oerley

cyaneum (Savigny)

Genus : *Eisenia* Malm em Michaelson

rosea f.typica (Savigny)

- *mut.macedonica* (Rosa)

For the permanganate treatments and soil cores, the mean of each species is shown in Table 3 p.28 as the number per locus and square metre. These are the same for the two permanganate treatments but not for the soil cores where the average per locus equals only 1/7th.of a square metre.

The soil cores taken after the permanganate treatments are not shown in Table 3, since their numbers by species are too small to be of value. Full details of the numbers of each species obtained by the different treatments are given in Appendix 2.

TABLE 3

AVERAGE NUMBER PER LOCUS AND SQUARE METRE

Species	1st. Perm. treatment Av.No.per Locus and sq. m.	2nd. Perm. treatment Av.No.per Locus and sq. m.	Soil Cores	
			Av.No. per locus	Av.No. per sq.m.
L.castaneus	3.2	2.8	7.8	54.6
L.terrestris	5	9.1	9.3	65.1
A.caliginosa	5.2	5	11.1	77.7
A.terrestris	19.8	8.3	21.4	149.8
O.cyaneum	.2	.5	1.5	10.5
E.rosea	1.6	3.7	12.85	89.95
Total	35	29.4	63.95	447.65

Discussion.

While the fifty soil cores, completing 1.43 square metres, produced 639.5 worms, the permanganate samples of 10 square metres, produced only 350 worms. Thus it is abundantly clear that the permanganate technique gave an unsatisfactorily low population estimate although of the same order as those of Evans and Guild (Evans and Guild,1947b,1948a,b, and Guild, 1948,1951a,b and 1952a and b).

The ten soil cores taken after the permanganate treatments produced 80.5 worms. These samples plus the loss by the permanganate treatments (1/35th.of total) fall within the range given by the soil cores from the unaffected.areas.

To determine whether or not the techniques extracted similar species ratios, analyses of variance were calculated for treatment pairs. The percentage of species per locus was used for this purpose and the results, as Snedecor's F, (Snedecor 1946) are given in Table 4 p.30. An example of the method is shown in Appendix 3.

TABLE 4

ANALYSIS OF VARIANCE - SNEDECOR'S F.

Species	Soil Cores v. Permanganate 1.		Soil Cores v. Permanganate 1 and 2	
	Between treatments d.f.1:9	Between samples d.f.9:9	Between treatments d.f.1:9	Between samples d.f.9:9
L.castaneus	4.35	2.41	2.35	2.08
L.terrestris	.0	.74	11.28	.99
A.caliginosa	2.48	2.41	.69	2.82
A.terrestris	53.81	1.46	16.33	1.87
O.cyaneum	2.86	.90	4.20*	3.06
E.rosea	61.66	1.61	52.72	4.41*

\- Significant at the 1% level.

* Significant at the 5% level.

In no case is there significant variance, at the 1% level, between samples which suggests an even distribution of the earthworm population and an intrinsic consistency of sampling method. Although all the techniques are consistent by themselves, they differ when compared with each other and in three species significant variance occurs between treatments. Thus relative to the proportion from the soil cores, the first permanganate treatment produced more specimens of Allolobophora terrestris and fewer Eisenia rosea than expected. Conversely, the second permanganate treatment produced more specimens of Lumbricus terrestris and fewer Eisenia rosea. Similar results were obtained by Satchell (1955a) in comparing the electrical method with the permanganate technique. This correlation of effect with species is interesting in suggesting that potassium permanganate, in conjunction with a hand sorting method, may be useful in determining the habits of different species.

The evidence discussed above and the results obtained by other authors by digging soil samples (Table 1 p.21) suggest that the permanganate technique is unsuitable for comparative population studies.

Some workers, however, using a soil sampling technique have also obtained very low population estimates. Many of these poor figures may be explained by assuming inefficient hand sorting; this must be meticulously done to achieve full results. Under optimum conditions, light soil, sparse vegetation and poor populations, it is suggested that a minimum of 2 days is necessary to sort 1 square metre to a depth of 20cms. Dreidax (1931), however, sorted 84 square metres to depths varying from .5 to 1.8 metres in one 'season'.

Thus in spite of low estimates quoted in Table 1 p.21 it is considered that permanent pasture in Europe will prove to average hundreds rather than tens of Lumbricids per square metre.

PART II

THE BIOLOGY OF THE LUMBRICIDAE ASSOCIATED WITH SHEEP DUNG AT MOOR HOUSE.

Introduction.

Fenton (1947) has suggested that more is known of the biology of the Lumbricidae than of other soil living groups but while this may be true very little information is available about individual species of the family. An important subdivision was made by Bornebusch (1930) who split the species he studied into surface, medium and deep living groups each with particular feeding habits. This author also considered that pigmentation was a characteristic of some species active on or at the soil surface. With the exception of *Lumbricus terrestris*, the pigmented species are often linked with habitats of a high humus content such as dung, rotting logs etc.. (Bornebusch,1930, Cernosvitov and Evans,1947 and Laurence, 1954)

Of the seven pigmented species found at Moor House six are associated with dung in that they commomly occur in the dung of their typical environments (Part III,pp.142-159).

These species are :- Lumbricus festivus, castaneus and rubellus, Dendrobaena octaedra and rubida and Bimastus eiseni.

This part of the study is concerned with field experiments and observations designed to give information on the biology of these species.

I. The Habitat - Dung.

Dung as a habitat for larval insects has béen described by many workers. (Laurence,1954 for a brief review.) Most of this work has dealt with cow dung whose condition and age has been shown to be important in deciding the order of invasion by insect species. No similar work is known on dung as a habitat for Lumbricidae.

Sheep dung is the usual type available to Lumbricidae at Moor House although some horse dung occurred mainly near the house.

The condition of the naturally available dung appeared to have more influence on its invasion by the Lumbricidae than did its type. Newly deposited sheep or horse dung was not invaded until it had 'aged' for anything up to 14 days. This period of 'aging' is thought to be varied by the effects of temperature and rainfall but has not been investigated in detail. The 'dry chip' state described by Mohr (1943) is infrequent at Moor House because of high rainfall (65 to 110 inches per year during the period of study). The dung does, however, lose 'body' when it lacks cohesion and may be more easily scattered by rain or wind; in this condition it rarely contains worms.

In the experiments discussed below sheep, cow and horse dung, either mixed or separately, was used and changed when it reached the unsuitable condition described above.

II. The Build-up of Lumbricidae Populations in Dung.

The bulk of the Moor House Reserve is covered by a blanket of peat and under these acid conditions Lumbricidae are too infrequent to be found by normal soil sampling techniques. Nevertheless, much of the sheep dung present was seen to contain worms suggesting aggregation from the surrounding area.

1. Aggregation into a Constant Supply of Dung.

Methods

An area of *Calluna* dominant moor (5 x 10 metres) was searched and cleared of dung, then the vegetation was mapped and fifty soil samples (PartI p.22) of 1/25th. of a square metre surface area were taken at random. At the intersections of a 1 square metre grid, 66 pieces of dung of approximately 300ccs. each were laid (Sept.1952) and examined at intervals during the next two years. The dung was replaced periodically when it became unsuitable (p.36).

The area was designated Experimental Site 2 and its position is shown on the map in Appendix 4 and described in Appendix 7.

Results.

In the initial search of the 50 square metres of the site 8 pieces of dung were found of which 4 contained 8 specimens of Dendrobaena octaedra. One immature specimen and one oötheca of Dendrobaena octaedra were obtained from the fifty, 20cm. cubed, soil samples.

Table 5 p.39, shows the total numbers of worms obtained from each of the 66 dung positions from the 31st. December 1952 to the 31st. December 1953 and Table 6 p.40 the same for 1954 (These Tables are given in a pattern of 11 x 6 totals showing the relative positions in which the dung was laid).

Table 7 p.41 shows the total number by species obtained from the site at each visit in 1953 and Table 8 p.42 the same for 1954. The number of oöthecae found are not given in Table 7 since only in 1954 was a high proportion extracted by a sufficiently exhaustive search of the dung.

TABLE 5

TOTAL NUMBER OF WORMS OBTAINED FROM EACH PIECE OF DUNG IN EXPERIMENTAL SITE 2

1953

							Total
	11	5	3	1	17	16	53
	4	1	5	7	24	54	95
	0	2	1	1	11	14	29
	5	3	3	5	6	8	30
	0	0	1	2	61	20	84
	2	3	0	0	11	6	22
	2	0	1	0	3	9	15
	0	1	0	2	7	2	12
	4	1	0	1	9	4	19
	9	0	3	1	4	4	21
	1	2	3	2	7	6	21
Total	38	18	20	22	160	143	401

TABLE 6

TOTAL NUMBER OF WORMS OBTAINED FROM EACH PIECE OF DUNG IN EXPERIMENTAL SITE 2

1954

							Total
	15	8	3	20	37	21	104
	32	13	4	11	30	20	110
	0	9	14	13	12	14	62
	4	6	1	2	20	29	62
	5	6	0	5	28	73	117
	4	4	1	8	4	24	45
	4	2	0	3	5	26	40
	0	2	0	9	22	20	53
	4	0	3	3	10	4	24
	3	1	6	6	5	4	25
	8	4	2	17	4	5	40
Total	79	55	34	97	177	240	682

TABLE 7

NUMBER OF WORMS PER EXAMINATION OF EXPERIMENTAL SITE 2 DURING 1953

Date of visit	Bimastus eiseni		Dendrobaena octaedra		Total No. of Worms
	Mature	Immature	Mature	Immature	
24.1.53	2				2
7.3.53			3		3
18.4.53			10	4	14
7.5.53			8	10	18
*22.5.53			3	4	7
27.6.53	4	1	14	4	23
17.7.53	2	5	19	1	27
6.8.53		12	16	9	37
* 9.8.53		11	5	4	20
22.8.53	3	6	5	3	17
30.8.53	10	55	5	5	75
11.9.53	21	46	11	16	94
13.10.53	16	10	6	11	43
6.11.53	3	2	3	1	9
8.12.53	8	2	1	1	12
Total	69	150	109	73	401

* Dung replaced.

TABLE 8

NUMBER OF WORMS PER EXAMINATION OF EXPERIMENTAL SITE 2 DURING 1954

Date of Visit	Bimastus eiseni			Dendrobaena octaedra			Total No. of Worms
	Mat.	Imm.	Ob.	Mat.	Imm.	Ob.	
15.1.54	5		5			0	5
*20.3.54	3	4	17	2	1	13	10
7.4.54	5		0	1	6	0	12
9.5.54	5	2	0	19	15	0	41
14.5.54	5		4	15	19	0	39
21.5.54	2		0	9	24	0	35
2.6.54	2		0	11	22	0	35
29.6.54	3	4	8	21	21	2	49
6.7.54		1	9	8	6	6	15
* 7.7.54			9	4	2	4	6
18.7.54	13	22	6	9	10	5	54
16.8.54	4	83	8	24	91	2	202
3.9.54	7	38	10	13	53	8	111
16.9.54	5	17	3	8	14	1	44
7.10.54	3	1	3	5	2	5	11
10.11.54	7	3	6		1	1	11
22.12.54		2	3			2	2
Total	69	177	91	149	287	49	682

* Dung replaced.

Discussion.

Tables 5 and 6 indicate that there are considerable differences in the numbers of animals obtained from the individual pieces of dung. The ranges were 0 - 61 in 1953 and 0 - 73 in 1954.

The position of those pieces of dung which produced no worms were the same for both years studied. These positions were normally waterlogged and it is concluded that the worms could not tolerate such conditions. Apparently few other organisms could live in this dung for it retained its fresh appearance and smell indefinitely.

Aggregation is apparent in both years in the North East corner of the site (upper right hand corner of Tables 5 and 6) and to a lesser extent in the outside pieces of dung.

This aggregation may be a result of, either movement into the dung from the surrounding area or the development of a population in situ. Working with different species, Evans and Guild (1948a) have shown that the production of oöthecae is increased with a good food supply such as dung and that several young per oötheca may be hatched in some species. Thus, it is possible that a rapid growth of population may occur in dung. The length of time necessary to reach maturity has not been investigated in *Dendrobaena octaedra* or *Bimastus eiseni* but approaches a year in other species (Evans and Guild,1948a). Therefore, under the conditions of examination the mature specimens found may be assumed not to have developed in situ.

In 1953, 178 or 44.39% of the 401 and in 1954, 218, or 31.96% of the 682 worms were mature. The difference in the proportion of mature animals in the two years is significant but results from a change in one species only. The proportion in the two species for both years are compared below in Tables 9 and 10 which include the results of analysis as a 2 X 2 contingency table.

TABLE 9

Bimastus eiseni

	Mature	Immature	Total
1953	69	150	219
1954	69	177	246
Total	138	327	465

χ^2 = 00.661 p = .30

TABLE 10

Dendrobaena octaedra

	Mature	Immature	Total
1953	109	73	182
1954	149	287	436
Total	258	360	618

$\chi^2 = 34.85$ $p = .001$

The number of oöthecae as a proportion of the numbers of mature animals for 1954 is given in a similar fashion in Table 11.

TABLE 11

	Bimastus eiseni	Dendrobaena octaedra	Total
Mature	69	150	219
Oöthecae	91	49	140
Total	160	198	358

$\chi^2 = 37.19$ $p = .001$

Thus, although Dendrobaena octaedra produced more young in 1954 than Bimastus eiseni it apparently did so from a smaller output of oöthecae. This difference is unlikely to have resulted from a relative failure to find the oöthecae of *D. octaedra* since they are white and more easily seen in this than other species.

Small numbers of the oöthecae of the two species were hatched separately and the number of young per oötheca recorded.

TABLE 12

Species	No. per oötheca 1	2	3	4	Total oothecae	Total worms
D. octaedra	13	1	0	0	14	15
B. eiseni	11	8	1	3	23	42

There is, therefore, a difference between the species but since *D. octaedra* produced less worms per oötheca than *B. eiseni*, it fails to explain the effect shown above. The apparent low production of oöthecae by *D. octaedra* is explained, however, if it lays a smaller proportion in the dung itself than does *B. eiseni*. This would also account for the differences between species in their proportions of immature specimens, since as a result of the removal of oöthecae from dung proportionately less specimens of *B. eiseni* would be allowed to develop.

The chance of a piece of dung being invaded by a worm moving in from outside the area will be influenced by the position of the dung within the grid. Thus, dung forming the outside of a grid should trap more worms than that of the centre.

Three rings are distinguished; ring 1, the dung of the outside of the grid; ring 2, that in an intermediate position and ring 3, that on the inside of the grid. Since the northern edge of the site (Top of tables 5 and 6) was adjacent to a peat hagg the grid is considered to be continuous at this point. Those pieces of dung are not included which were commonly waterlogged leaving 24 pieces in ring 1, 19 in ring 2 and 14 in ring 3.

The number of occasions when worms were found in these rings is given in Table 13, p.48 for the 15 examinations of 1953 and in Table 14, p.48 for the 17 of 1954.

These results, averaged as the numbers per 20 pieces of dung, are shown as cumulative graphs; for 1953, Fig.3 p.49 and for 1954, Fig.4 p.50.

THE NUMBER OF PIECES OF DUNG WITH WORMS IN OUTER, MIDDLE AND INNER RINGS, EXPERIMENTAL SITE 2

TABLE 13

Ring	Series of examinations 1953															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1.	0	0	8	6	4	5	11	13	3	5	6	14	10	4	4	93
2.	1	2	4	5	1	7	6	4	6	6	7	8	11	1	1	70
3.	1	1	0	0	2	0	3	4	1	0	3	6	1	2	5	29

TABLE 14

Ring	Series of examinations 1954																	Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1.	1	3	3	7	9	9	10	17	6	2	14	17	15	14	5	5	0	137
2.	2	1	5	7	6	7	7	8	6	1	10	17	16	6	2	3	1	105
3.	2	1	1	8	3	5	4	5	2	2	6	8	8	3	4	0	0	62

FIG. 3.

Presence of Lumbricidae Recorded in Outer, Middle and Inner Rings of Dung, Experimental Site 2.

1953

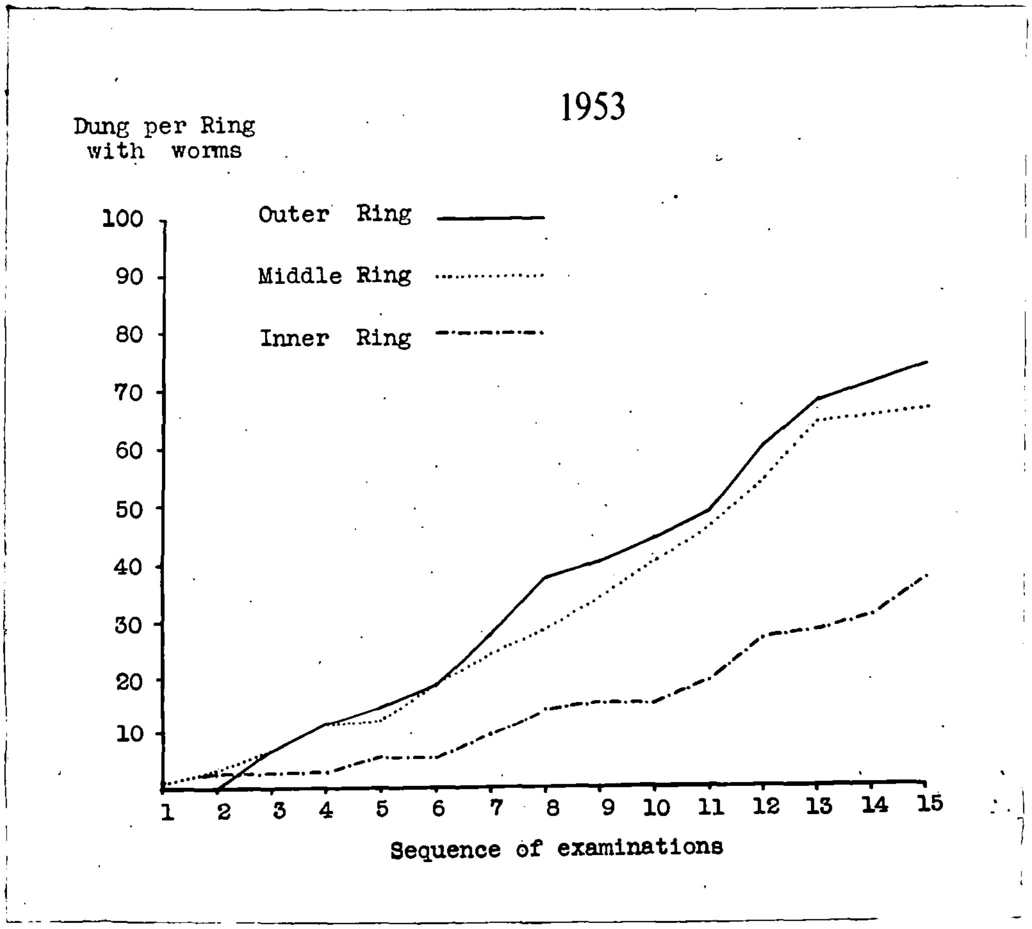
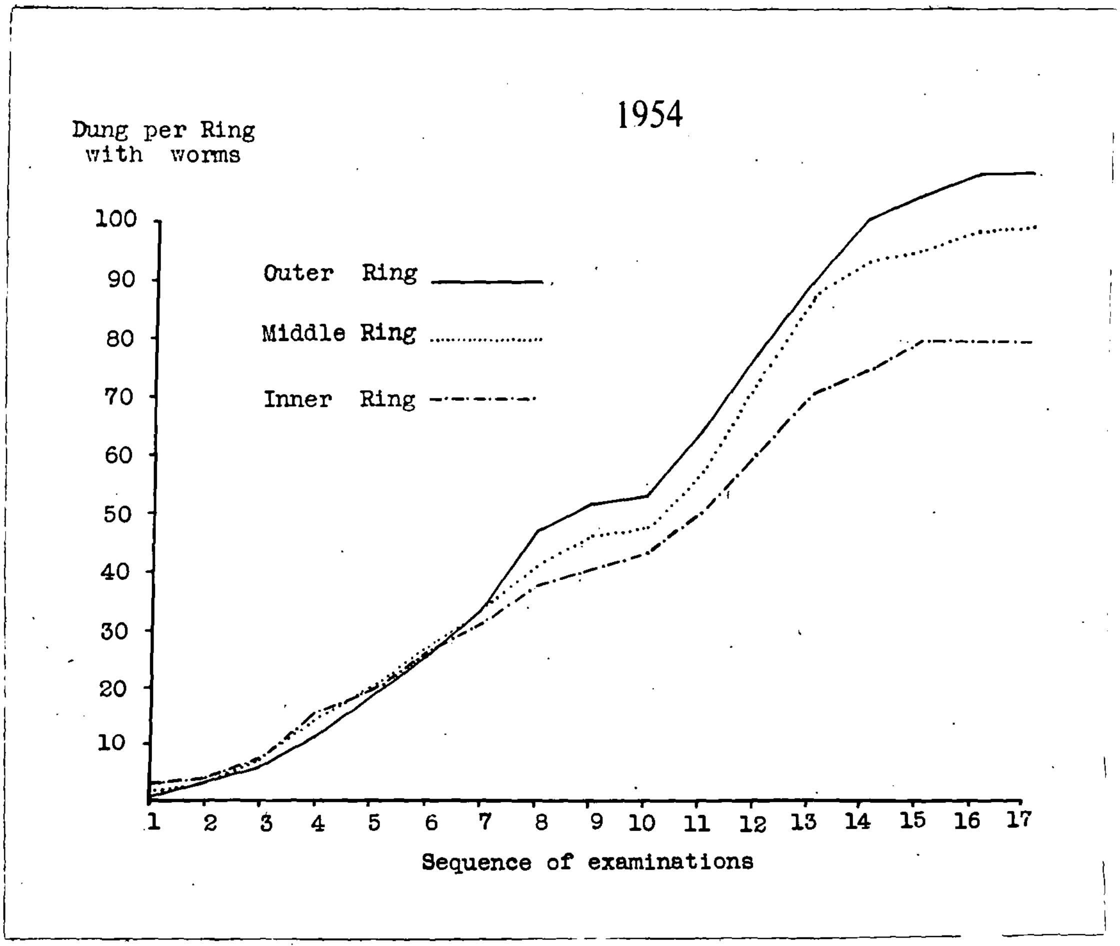


FIG.4.

Presence of Lumbricidae Recorded in Outer, Middle and Inner Rings of Dung, Experimental Site 2.

1954



In the first part of 1953 there is no difference between the rings. This is as expected since the dung is then being invaded by the worms already present on the site. Later the totals found in the rings diverge and ring 3 is markedly less invaded than the others.

In 1954 the similarity of the three rings is continued much longer than in 1953; an indication of the population in situ as a result of the activity in that year. Again, however, the three rings diverge later in the year because of the period of high activity of late summer.

2. Experimental studies using dung spaced at different intervals

It was thought that a comparison of the aggregations found in dung spaced at different intervals would give some measure of the effective area of attraction if this were larger than that covered by the dung itself. Some attempt was also made to investigate the length of time Lumbricidae spent in dung.

Methods.

In 16 places (experimental sites 3 - 11, 15 and 19 - 24) dung was laid spaced in three patterns. Each piece of dung was of 300ccs. and the patterns were:-

Long line: 11 pieces of dung laid in a straight line each piece 1 metre apart.

Square: 16 pieces of dung laid on a 30cm. grid covering an area of 1 square metre.

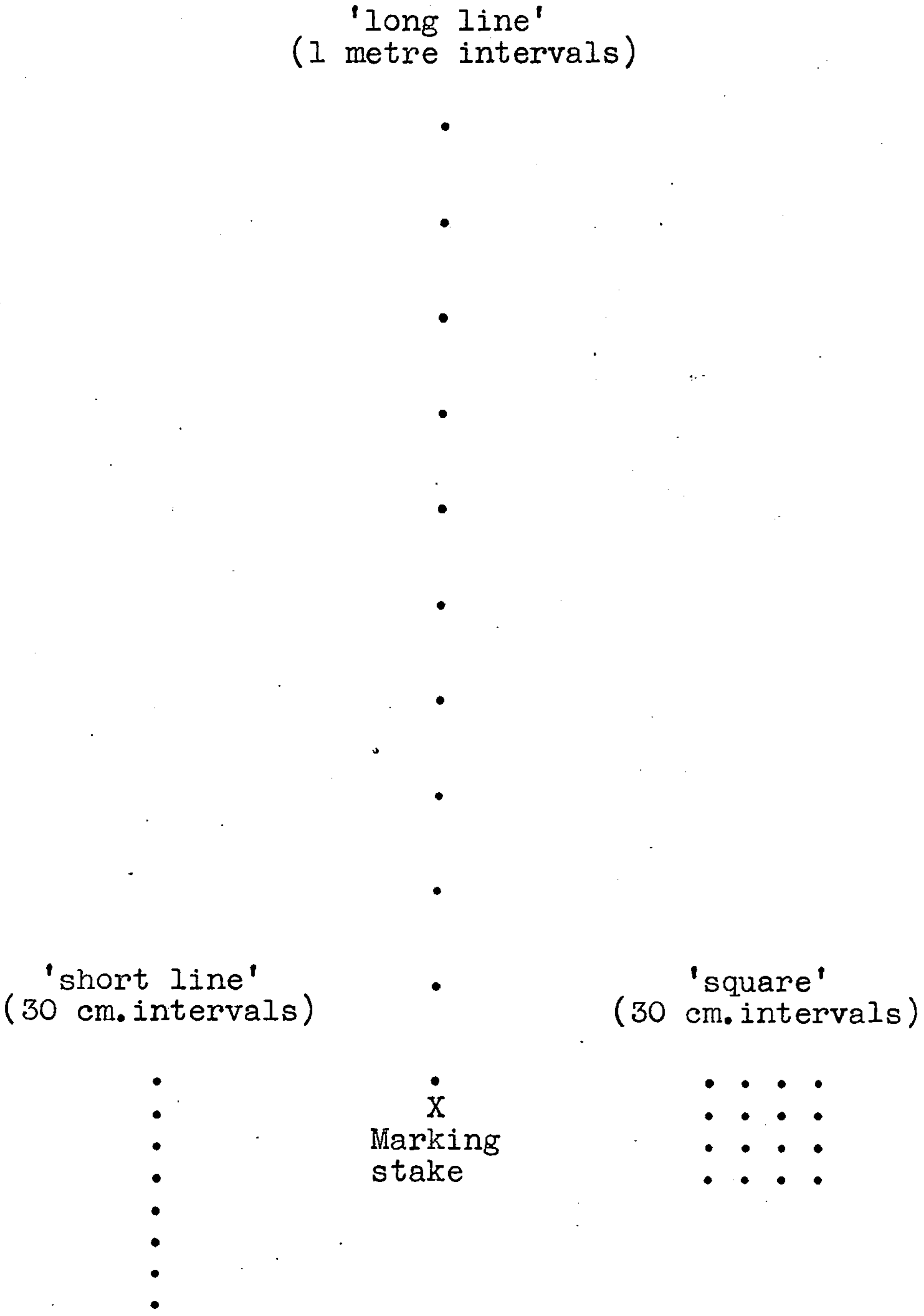
Short line: 8 pieces of dung laid in a straight line each piece 30cm. apart.

A diagram of these patterns is given in Fig.5,p.53, and the site positions shown on the map in Appendix 4 and described in Appendix 7.

FIG. 5

THE PATTERNS OF DUNG USED IN EXPERIMENTAL SITES

3 - 11, 15 AND 19 - 24



The patterns were separated by 2 metres at their nearest points and the position of each piece of dung known by its proximity to a marked stake. The sites were examined periodically during 1953 and the worms removed from the 'long line' and the 'square'. Those found in the 'short line' were recorded and then replaced. Examination of the 'short line' and 'square' was not continued in 1954. The site environments and results for 1954 are not described here since only the effects of the patterns are relevant to the present discussion.

Results

The total number of worms obtained from the dung of the 'long lines' and 'squares' during 1953 is given in Table 15, p.55 and for direct comparison the numbers from 'squares' reduced to 11/16th. are included.

Of those sites visited on a number of occasions, records of interest were made in the 'short lines' of sites 5,7,9 and 11. The occurence of worms and oöthecae in these patterns on the dates of examination is shown in Table 16, pp.56 and 57.

TABLE 15

TOTAL NUMBER OF LUMBRICIDAE RECORDED FROM DUNG OF EXPERIMENTAL SITES 3-11, 15 and 19-24 IN 1953

Site No.	No. of visits	'Long line' 11 pieces of dung	'Square' 16 pieces of dung	11/16ths. of 'Square' total
3	9	1	0	0
4	8	1	2	1.38
5	8	13	4	2.75
6	8	0	0	0
7	9	0	0	0
8	9	1	0	0
9	9	15	2	1.38
10	9	54	24	16.5
11	9	4	3	2.06
15	7	42	18	12.38
19	2	32	19	13.06
20	2	13	24	16.50
21	2	0	0	0
22	2	28	54	37.13
23	2	278	129	88.69
24	2	116	110	75.63

TABLE 16

RECORDS FROM THE DUNG OF 'SHORT LINES'

Date of visit	Experimental site 5 Dung number 1	2	3	4	5	6	7	8
24. 6.53						?		
17. 7.53				B.e.				
5. 8.53				? 1 oö			?	
24. 8.53	D.o.							
30. 8.53								
11, 9.53								
6.11.53								
8.12.53								
	Experimental site 9							
28. 6.53								
18. 7.53		B.e.						B.e. 1 oö
5. 8.53		B.e.						
23. 8.53	B.e. 1 oö	3 oö						2 oö
29. 8.53	2 oö							
13. 9.53	1 oö					1 oö		
12.10.53						B.e.		
6.11.53						B.e.		
9.12.53	2 oö			?				1 oö

D.o. = <u>Dendrobaena octaedra</u> B.e. = <u>Bimastus eiseni</u>

? = Immature specimen, species unknown

oö = <u>Bimastus eiseni</u> oöthecae

TABLE 16 (Continued)

Date of visit	Experimental site 11 Dung number 1	2	3	4	5	6	7	8
28. 6.53								
18. 7.53								
5. 8.53	?							
22. 8.53								
29. 8.53								
12. 9.53								
12.10.53								
6.11.53								
9.12.53				B.e.				
	Experimental site 7							
27. 6.53								
17. 7.53					B.e.			
5. 8.53					B.e.			
22. 8.53					B.e.	?		
30. 8.53								
11. 9.53						1 oö		
9.10.53								
6.11.53								
8.12.53						?		

B.e. = <u>Bimastus eiseni</u>

? = Immature specimen, species unknown

oö = <u>Bimastus eiseni</u> oöthecae

Discussion

The effect of patterns

In sites 1 - 11 and 15 the populations were low and the sites examined a number of times. The total obtained from the 'long lines' of these sites invariably exceeds that from the 'squares'. Thus, the effective attraction of the dung is increased by its separation either as a result of the suggested movement of the worms or the increased chance of the 'long line' pattern contacting a pre-existing aggregation. The number of replications are not sufficient to distinguish these possibilities.

In sites 22 - 24 the number of worms obtained from the 'square' is large enough for a comparison of the effect of the position of the dung.

Twelve of the sixteen pieces are on the outside of the square and can be assumed to have more chance of trapping worms than the four pieces of the centre. The proportions of the total worms found by these two parts of the pattern are compared in Table 17,p.59, where the total from the outer dung has been divided by three to make it comparable with that from the centre.

TABLE 17

	Site 22	Site 23	Site 24	Total
Centre	7	25	15	47
Outside	15.66	34.66	31.66	81.98
Total	22.66	59.66	46.66	128.98

$\chi^2 = 1.44$ $p = .30$

Thus, the number of worms obtained from the outside dung is greater than that from the centre in a similar proportion in all three sites. This supports the inference of this section that invasion of dung by Lumbricidae is a result of movement greater than that necessitated by entrance from the soil immediately beneath the dung.

The length of time Lumbricidae spend in dung

The records from 'short lines' given (Table 16,pp.56 and 57), are those from areas where the total population was so low that it could be reasonably assumed that any worm recorded in consecutive examinations was the same individual. On this assumption three of the nine mature (therefore, recognisable in the field) worms recorded stayed in the dung any length of time.

1 E.S.7 Bimastus eiseni at least 37 days.

2 E.S.9 Bimastus eiseni at least 19 days.

3 E.S.9 Bimastus eiseni at least 26 days.

The records of mature Bimastus eiseni were often followed by records of their oöthecae which supports the suggestion made above (p.46) that this species lays a high proportion of its oöthecae in dung. Dendrobaena octaedra was only recorded once in this case so that a comparison between the species cannot be made.

III. Field experiments on the methods of entrance to dung

Methods

A series of treatments were designed in which either entrance to the dung or its flow of products was restricted.

Entrance to dung was restricted; from beneath by a gauze plate; from the surface by a gauze ring and by an artificial surround, dung on the surface of a tile. The effect of the dung products was measured; by carrying products deep into the soil in a funnel and by comparing results from beneath a control tile without dung to that with dung. The importance of dung volume was assessed by a comparison of half and twice a standard volume with the standard.

Two series of experiments were made; at one site in 1953 (experimental site 18) and at six in 1954 (experimental sites 27 - 32). In all cases unless otherwise stated; the volume of dung was 300ccs.; the treatment positions were one metre apart and the sites were examined daily for periods terminated when any of the treatments began to show wear.

Other sites, 17 and 25 - 6, of a similar type were in areas of low population but failed to produce sufficient numbers for a satisfactory analysis of results.

Details of the treatments are given below.

1953

A pilot experiment of seven treatments (E.S.18) was examined for one period. The seven treatments were:-

1. Normal dung N. (5 replications) a control of 300ccs. of dung.
2. Dung on tile T+. (5 replications) dung placed on top of a floor tile, 15cm. square and 2cm. thick.
3. T-. (5 replications) the area beneath the tile plus dung, T+.
4. Gauze plate G. (5 replications) dung laid on a phosphor-bronze gauze plate (1mm. mesh) of 10cm. diameter. The dung covered the gauze plate completely.
5. T. (5 replications) The area beneath a floor tile without dung.
6. Funnel (3 replications) dung laid on a gauze plate over a funnel (10cm. diameter) sunk flush with the ground. The stem of the funnel was

extended by first sinking a length of pipe into the ground making the effective outlet more than 20cm.deep.

7. Ring R.(5 replications) dung laid inside a gauze ring of 10cm.diameter. The ring was sunk into the ground 2cm. and extended above the surface 10cm.

1954

For three periods in June, September and October 1954 the experiment was repeated on six sites (E.S.27 - 32) with three replications of eleven treatments. The treatments modified and added to the 1953 experiment are detailed:-

1. Normal dung N. as for 1953.
2. Half normal dung 1/2N. 150ccs. of dung.
3. Twice normal dung 2N. 600ccs. of dung.
4. Dung on tile T+. as for 1953.
5. Beneath tile plus dung T-. as for 1953.
6. Beneath tile without dung T. as for 1953.
7. GT+. as for dung on tile T+, but with a 4cm. deep strip of perforated zinc, surrounding the tile, sunk 2cm. into the ground and not extending above the tile surface.

8. GT-. as for T-, but the area beneath the tile and within the zinc strip of GT+.

9. Gauze plate G. dung placed on a plate of perforated zinc over a funnel sunk flush with the ground. The funnel was blocked with soil before the dung was placed. The diameter of the funnel and plate was increased to 15cm. and the dung did not, therefore, reach its edge.

10. Funnel F. as for 1953 but with the 15cm. funnel and a perforated zinc plate.

11. Ring R. as for 1953 but of perforated zinc and a diameter of 15 cm. (Plate 3 p.65).

<u>Results</u>

The totals by species for the seven treatments of E.S.18 are given in Table 17, p.66. Since there were only three replications of treatment F. compared to the five of other treatments the totals for F. have been multiplied by 1.4 for ease of comparison.

The totals for eleven treatments and three replications are given for the six sites, 27 - 32. in Tables 19 - 24, pp.67 - 72. The total numbers by species for these sites are given in Table 56, Pt.III, p.157 .

PLATE 3.

1954 Treatment R. - Ring Round Dung Preventing

Access at the Soil Surface.

TABLE 18

TOTALS BY SPECIES FOR TREATMENTS IN EXPERIMENTAL SITE 18

Species	N.	T-.	T+.	T.	G.	R.	F.	Total
L.rubellus	104	87	25	7	95	22	50	390
L.festivus	4	4				1		9
D.octaedra	3				2		1	6
D.rubida	25	16			26	20	6	93
O.cyaneum		1						1
A.chlorotica	2	8		1	1	15		27
A.caliginosa	1	4				2		7
E.rosea	1	1						2
E.tetraedra	2				1		1	4
Total	142	121	25	8	125	60	58	539

TABLE 19

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 27

Treatments	Replications 1	2	3	Total
N.	25	52	20	97
T-.	9	20	46	75
T+.	10	12	1	23
1/2N.	10	10	19	39
GT-.	9	17	14	40
GT+.	4	8	7	19
2N.	77	28	56	161
T.	2	0	9	11
G.	4	4	8	16
F.	4	0	7	11
R.	29	3	4	36
Total	183	154	191	528

TABLE 20

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 28

Treatments	Replications 1	2	3	Total
N.	26	33	44	103
T-.	20	22	39	81
T+.	6	4	5	15
1/2N.	5	15	18	38
GT-.	23	18	31	72
GT+.	2	10	6	18
2N.	47	47	40	134
T:	11	6	2	19
G.	5	12	5	22
F.	4	0	2	6
R.	2	6	3	11
Total	151	173	195	519

TABLE 21

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 29

Treatments	Replications 1	2	3	Total
N.	37	51	54	142
T-.	21	35	57	113
T+.	6	20	19	45
1/2N.	21	83	27	131
GT-.	8	58	41	107
GT+.	1	31	13	45
2N.	19	153	100	272
T.	6	32	19	57
G.	7	43	14	64
F.	7	1	6	14
R.	17	11	5	33
Total	150	518	355	1,023

TABLE 22

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 30

Treatments	Replications 1	2	3	Total
N.	5	9	6	20
T-.	4	10	2	16
T+.	3	1	6	10
GT-.	11	0	22	33
GT+.	2	4	10	16
2N.	11	34	62	107
T.	0	2	13	15
G.	3	4	9	16
F.	0	1	3	4
R.	6	3	4	13
Total	51	73	146	270

TABLE 23

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 31

Treatments	Replications 1	2	3	Total
N.	20	35	33	88
T-.	11	5	11	27
T+.	9	17	8	34
1/2N.	8	9	11	28
GT-.	8	11	15	34
GT+.	12	18	22	52
2N.	41	48	47	136
T.	2	1	2	5
G.	11	28	11	50
F.	6	8	7	21
R.	10	6	7	23
Total	138	186	174	498

TABLE 24

THE LUMBRICIDAE FROM THE TREATMENTS AND REPLICATIONS OF EXPERIMENTAL SITE 32

Treatments	Replications 1	2	3	Total
N.	50	37	45	132
T-.	17	25	24	66
T+.	12	32	2	46
1/2N.	17	27	21	65
GT-.	16	25	15	56
GT+.	7	13	13	33
2N.	79	64	85	228
T.	4	11	4	19
G.	14	21	18	53
F.	2	4	3	9
R.	5	8	5	18
Total	223	267	235	725

1. Statistical analysis of the results from Experimental sites 27-32 (Tables 19-24)

To demonstrate the possible effect of the sites and replications on the treatments.

Items	=	x
Eleven treatments	=	a
Six sites	=	b
Three replications	=	c
Sum of number per replication	=	R
Sum of number per site	=	S
Sum of number per treatment per site	=	t
Sum of number per treatment	=	T
Sum of items	=	G

Then :-

$$\text{Correction} = \frac{G^2}{abc} = 64{,}116.00$$

$$\Sigma_1 = \frac{S_1^2 + S_2^2 \;\ldots\ldots\; S_6^2}{ac} - \text{Correction} = 9{,}859.85$$

$$\Sigma_2 = R_{1,1} + R_{1,2} \;\ldots\; + R_{6,3}$$

$$- \text{Correction} = 16{,}856.27$$

$$\Sigma_3 = \frac{(R_{1,1} + R_{2,1} + R_{3,1} \ldots)^2 + \ldots\ldots + (\ldots + R_{5,3} + R_{6,3})^2}{ab}$$

$$- \text{Correction} = 1{,}976.01$$

$$\text{Error} = \Sigma_1 - \Sigma_3 \qquad = 5{,}020.41$$

	Sum of Squares	d.f.	Mean of Squares	F
Between sites	9,859.85	5	1,971.97	3.92
Between replications	1,976.01	2	988.01	1.9
Error	5,020.41	10	502.04	
Total	16,856.27	17		

Since there is no significant effect on the treatments by either the sites or the replications they may be summed and the analysis continued.

To demonstrate differences between treatments.

$$\Sigma_4 = \frac{T_1^2 + \ldots\ldots\ldots + T_{11}^2}{bc}$$

$$- \text{Correction} = 43{,}071.39$$

$$\Sigma_5 = t_{1,1}^2 + t_{1,2}^2 + \ldots + t_{6,10}^2 + t_{6,11}^2$$

$$- \text{Correction} = 61{,}569.67$$

$$\Sigma_6 = \Sigma_5 - \Sigma_4 - \Sigma_1 \qquad = 8,638.43$$

$$\Sigma_7 = \Sigma x^2 - \text{Correction} \qquad = 84,106$$

$$\text{Error} = \Sigma_7 - \Sigma_6 - \Sigma_4 - \Sigma_2 \qquad = 15,539.91$$

	Sum of Squares	d.f.	Mean of Squares	F
Whole block	16,856.27	17		
Between treatments	43,071.39	10	4,307.14	33.26
Sites X treatments	8,638.43	50	172.77	1.33
Error	15,539.91	120	129.50	
Total	84,106.00	197		

The difference between treatments is highly significant and may be examined by the standard error of the treatment means which equals :-

$$\sqrt{\text{of } \frac{129.5}{9}} = 3.794$$

The treatment means are :-

Normal dung	N.	582 ÷ 18	= 32.33
Beneath tile plus dung	T-	378	= 21.00
Dung on tile	T+	173	= 9.61

Half normal dung	1/2N.	321	= 17.83
Beneath tile with gauze ring plus dung	GT-.	342	= 19.00
Dung on tile with gauze ring	GT+.	183	= 10.17
Twice normal dung	2N.	1,038	= 57.66
Tile without dung	T.	126	= 7.00
Gauze plate	G.	221	= 12.28
Funnel	F.	65	= 3.61
Ring	R.	134	= 7.44

<u>To demonstrate the effects of some treatments on the proportions of mature/immature specimens found</u>

The proportion of mature animals per treatment was examined by Analysis of Variance for the five treatments, N., 1/2N., 2N., T-., and T+. with the following result.

	Sum of Squares	d.f.	Mean of Squares	F
Between sites	.3229	5	.0645800	5.82
Between treatments	.4667	4	.1166750	10.52
Residual	.221752	20	.0110876	
Total	1.011352	29		

There is a significant difference between the treatments. The treatment means and their standard error are shown :-

Normal dung	N.	= .2912
Beneath tile plus dung	T-.	= .5468
Dung on tile	T+.	= .1750
Half normal dung	1/2N.	= .2528
Twice normal dung	2N.	= .3147

Standard error = .01924

<u>To demonstrate the effect of some treatments on the proportions of four common species found</u>

The proportions of four species, <u>L.rubellus</u>, <u>D.octaedra</u>, <u>D.rubida</u> and <u>A.chlorotica</u> found by the treatments N., T-., T+., 1/2N., 2N. and R. were examined for each site by contingency tables.

An example of the results is given in Table 25, p.78, for the sum of three similar sites, 27, 28 and 32.

TABLE 25

TABLE OF χ^2 FROM A CONTINGENCY TABLE OF SPECIES PROPORTIONS

Species	N.	T-.	T+.	1/2N.	2N.	R.	Total
L. rubellus	1.07	2.20	4.41	1.99	.01	(14.11)	23.79
D. octaedra	3.76	2.73	.49	.20	.02	.10	7.30
D. rubida	1.34	1.21	.72	3.00	1.30	<u>24.36</u>	31.93
A. chlor.	(5.41)	<u>43.54</u>	(8.78)	.05	2.08	.72	60.58
Total	11.58	49.68	14.40	5.24	3.41	39.29	123.60

Large χ^2's as a result of a lower observed proportion than expected are bracketed while those from too high a proportion are underlined

2. <u>The movement into dung of pigmented and unpigmented groups of Lumbricidae</u>

Six pigmented and six unpigmented species were found by the experiment at sites 27 - 32 (Pt.III, Table 56 ,p. 157) but of the 3,563 worms only 292 or 8.2% belonged to the unpigmented group of species. Since the total includes those worms from the treatments 'beneath tiles' where some unpigmented species could be expected it is concluded that only the active pigmented group aggregate into dung.

Compared to the pigmented group a high proportion of the unpigmented species was found to be mature.

TABLE 26

	Mature forms	Immature forms	Total
Unpigmented group	153	139	292
Pigmented group	938	2,333	3,271
Total	1,091	2,472	3,563

$\chi^2 = 72.1 \quad p = .001$

This high proportion of mature specimens in the unpigmented group may follow from their activity at night (See p.98) which may also allow some aggregation in the soil beneath dung.

3. Aggregation in different volumes of dung

The only difference between N., 1/2N. and 2N. was in the amount of dung; 300, 150 and 600ccs. respectively. This, however, had the effect of producing a significantly greater number of animals with an increased amount of dung. The dung was examined daily and the worms removed so that it is difficult to believe that crowding would produce these differences.

The number of animals found are in a similar ratio to that of the volume of dung in the treatments, that is, a mean of 57.7 worms for 600ccs. of dung, 32.3 for 300 and 17.8 for 150. The ground surface covered by dung increases with amount but not to the extent of the differences observed.

No difference was found in either the species proportions or the proportions of mature forms in these three treatments (pp.76 - 78) and it seems that large volumes of dung are more attractive to all species and states than small volumes. The reason is obscure. It is possible that large volumes modify the effects of fluctuations in the external environment (Temperature and water loss) and 2N. may, therefore, have been most attractive because of the conditions existing during the experiment.

4. <u>The importance of dung products</u>

The aggregation in dung of some Lumbricid species indicates that it is an attractive habitat. The greater number of worms found under the tile with dung compared to the control without dung (Treatment means T-. 21.00 : T. 7.00) shows that the worms may respond to the dung products alone. Similarly, smaller numbers were obtained from the dung of treatment F. where the products were carried deep into the soil than from the control G. where more of the products remained on the surface(Treatment means F. 3.61 : G. 12.28).

The effect on the soil surface of the activity of Lumbricidae aggregated beneath the tile plus dung T-. is shown in Plate 4, p.82. A similar photograph, Plate 5, p.82, comtrasts the control T. without dung and here the vegetation is etiolated but very little disturbance of the soil has occurred.

PLATE 4.

Area Beneath Tile Plus Dung.

PLATE 5.

Area Beneath Tile Without Dung.

5. <u>The effect of barriers in preventing entrance to dung</u>

There was no significant difference between the numbers of worms obtained from the treatments, tile plus dung (T-. and T+) and the tile with gauze plus dung (GT-. and GT+). The treatment means were T+. 9.61 : GT+. 10.17 and T-. 21.00 : GT-. 19.00. The daily examinations quickly distorted the zinc strip of GT-. so that worms could pass freely beneath the tile. For this reason the treatment failed and can only be considered as a further replication of 'tile plus dung'.

The dung on top of tiles T+. produced smaller numbers of worms than the control of normal dung N. (Treatment means T+. 9.61 : N. 32.33). The sum of the means from beneath the tile plus dung and the dung itself is 30.61 which is similar to that of the control N. 32.33. Thus, the total attractiveness of the dung was similar but in reducing the number of worms entering T+. the tile acted either as a barrier or a more attractive alternative.

The ring R. prevented access to dung at the soil surface but not from beneath or at a depth of more than 2cm.. Significantly smaller numbers of worms were obtained from dung with this treatment than with the control N. (Treatment means R. 7.44 : N. 32.33) suggesting that entrance to dung is achieved at the soil surface rather than from beneath.

Entrance to dung from beneath but not at the surface was prevented by the blocked funnel treatment G. which produced a significantly smaller number than the control N. (Treatment means G. 12.28 : N. 32.33). However, if entrance to dung occurs mainly at the soil surface then the sum of the treatment mean of G. with that of R. should exceed the treatment mean of the control N.; this it fails to do (Σ G. and R. 19.72 : N. 32.33).

The totals from the pilot experiment of 1953 for these three treatments are R. 60, G.125 and N.142 so that here R.plus G. does exceed N.. The treatments 'G.' in the two years differed in that in 1954 there was an interval of approximately 2.5cm. between the dung and the natural soil surface and the soil beneath the plate had been disturbed in placing the blocked funnel. Thus, G. of 1954 may be more comparable with T+.(Treatment means G. 12.28 : T+. 9.61), the interval of tile or plate between the dung and natural soil surface acting as a barrier to entrance. Alternatively, the environment of these two treatments may have differed from the control N. in being less sheltered by surrounding vegetation. There was, however, no difference in the effect of sites or replications on treatments (p.74) although the amount of vegetation cover varied a great deal.

The possibility that Lumbricidae are so sensitive to the 'smell' of dung that the disturbance of placing the blocked funnel of G.1954 was sufficient to significantly reduce their chance of responding should not be overlooked. If this were so it might also account for the observed differences between dung volumes. Although such sensitivity seems unlikely in such a relatively simple animal there are many precedents in even simpler groups.

6. The effects of treatments on the proportions of species and mature/immature forms.

A significantly high proportion of mature/immature specimens and of the species Allolobophora chlorotica was found beneath the tile plus dung T-..

Conversely both proportions were significantly low in dung on top of tiles T+.(pp.76 - 78). The proportion of the unpigmented species _A.chlorotica_ is high beneath tiles with dung because to some extent this simulated a soil habitat (Plate 4,p.82) and for the opposite reason the proportion is low in dung on top of tiles. The reason for the high proportion of mature forms found beneath tiles with dung is obscure. The proportion may have been influenced to some extent by the relatively high numbers of _A.chlorotica_ (See p.79) but the effect was also observed in site 30 where this species did not occur.

A significantly high proportion of _Dendrobaena rubida_ and low proportion of _Lumbricus rubellus_ was found by the treatment R. which prevented access to the dung at the surface. This may reflect a difference of behaviour between the species. Alternatively, the distinction may be a result of the different size of the species in that the barrier was more effective to the larger _L.rubellus_.

IV. The distance covered in aggregating into dung

1. Attempts to mark Lumbricidae.

Release and recapture of marked individuals would have been a useful method of assessing the distances Lumbricidae move but no satisfactory method of marking worms was found.

An attempt was made to mark individuals by the excision of several hind segments. These cuts healed rapidly, however, and were not then readily detectable.

Small pieces of magnetized steel were introduced into the body cavity and the marked worms detected by their deflection of a compass needle. A high proportion of individuals marked in this way were severely damaged in the process, nor was the steel retained in the body for more than a few days.

Neither of these methods was used in a field experiment.

2. The isolation of populations of a known area

Since movement of Lumbricidae into dung is a result of surface activity, it was thought that areas could be isolated and movement of the population, without the complication of constant replenishments, measured by the distance the individuals were set to find dung.

Areas of 2 X 2 metres were isolated by means of ditches 20cm. wide. These were also 20cm. deep and they usually contained free water. The dung was laid out in the areas isolated, in three patterns.

1 piece of dung in the centre of an area of four square metres.

4 pieces of dung, one in the centre of each of the four square metres.

16 pieces of dung, four to each of the four square metres.

Two sites, E.S.33 (3 replications, dung deposited 24.6.1953) and E.S.34 (4 replications, dung deposited 9.8.1953) were examined in this way. The populations involved were low and examination of the dung was at approximately fortnightly intervals until the winter of 1953.

The total Lumbricidae from the replications of the three patterns of each site is shown in Table 27, p.89.

TABLE 27

THE TOTAL LUMBRICIDAE PER REPLICATION OF THE THREE DUNG PATTERNS OF EXPERIMENTAL SITES 33 and 34

1953

	Site 33			Site 34		
	Pieces of dung per pattern			Pieces of dung per pattern		
	1	4	16	1	4	16
Replication 1.	0	2	3	4	4	12
Replication 2.	0	1	1	3	17	24
Replication 3.	0	2	1	4	6	29
Replication 4.	/	/	/	1	8	8
Total	0	5	5	12	37	73
Average per piece of dung	0	.42	.10	3.0	2.31	1.14

More worms per piece of dung and fewer per area are found with a decreased number of pieces of dung.

Two sources of error may influence these results.

The possible effect of aggregations existing before the areas were isolated cannot be distinguished owing to the small number of replications used. Again, if the worms only stay in dung for short periods then the chance of finding worms at any one time will be increased with an increase in the number of pieces of dung examined. In spite of these possible errors it is concluded that the effective area of attractiveness of 300ccs. of dung is at least less than four square metres.

V. Lumbricid activity related to Temperature, Darkness and Rainfall

1. Activity related to Temperature

The effect of temperature on the activity of Lumbricidae as measured by their aggregation in dung may be assessed to some extent by the seasonal activity shown in records obtained throughout a year.

The dung of experimental site 2 was examined at irregular periods for more than two years and the numbers of mature and immature worms of the two species obtained in 1953 and 1954 are shown in a histogram, Fig.6, p.92. To overcome the effects of the irregular examinations the totals shown have been calculated as for 14 day periods throughout the year.

Discussion

The pigmented Lumbricidae aggregate into dung at the soil surface and are, therefore, liable to experience rapid fluctuations in temperature. The effect of these fluctuations at the soil surface may be overcome to some extent by burrowing into litter but such action would at the same time

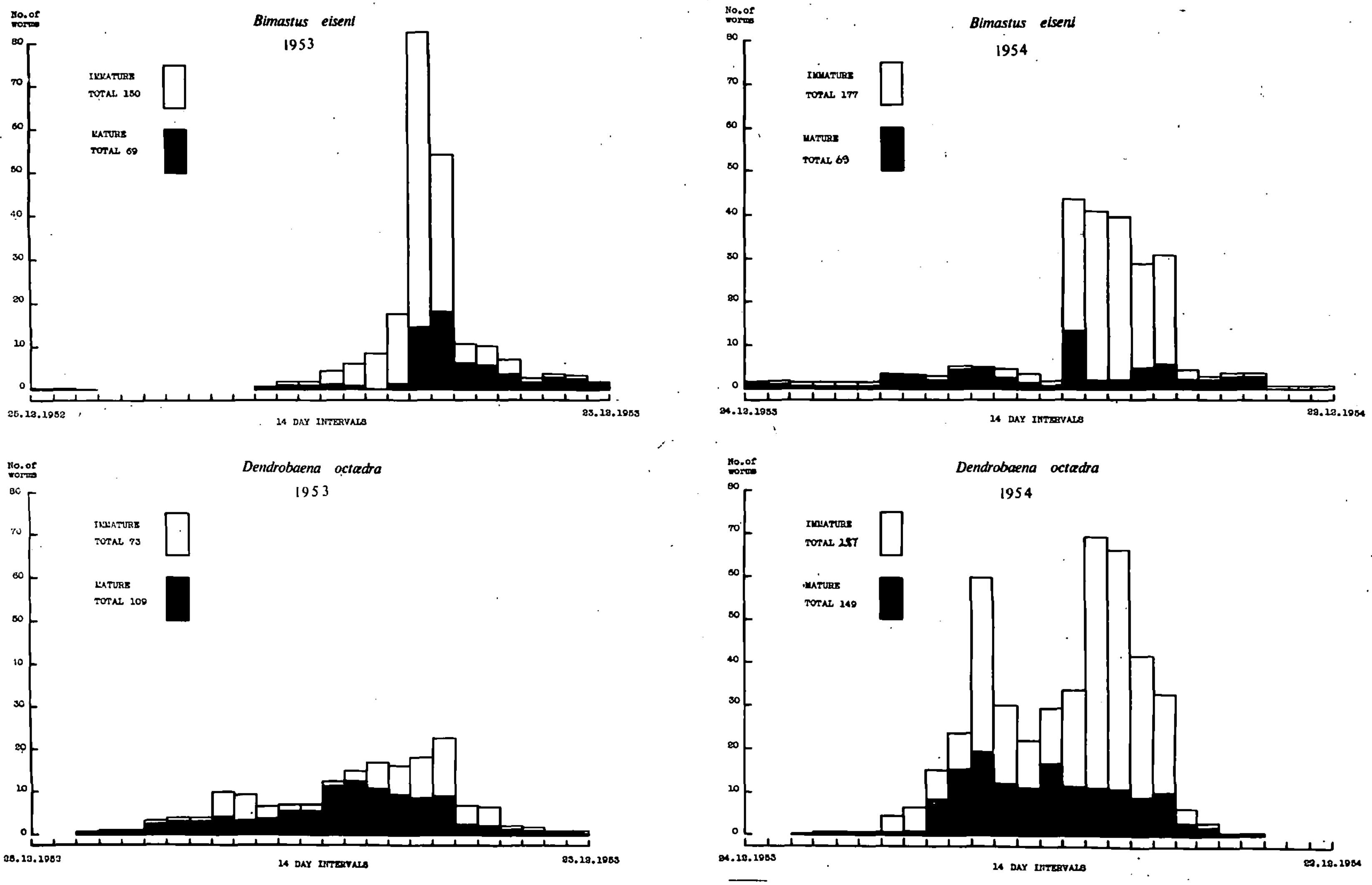

No. of worms
Bimastus eiseni
1953
IMMATURE
TOTAL 150
MATURE
TOTAL 69
25.12.1952
14 DAY INTERVALS
23.12.1953
No. of worms
Bimastus eiseni
1954
IMMATURE
TOTAL 177
MATURE
TOTAL 69
24.12.1953
14 DAY INTERVALS
22.12.1954
No. of worms
Dendrobaena octædra
1953
IMMATURE
TOTAL 73
MATURE
TOTAL 109
25.12.1952
14 DAY INTERVALS
23.12.1953
No. of worms
Dendrobaena octædra
1954
IMMATURE
MATURE
TOTAL 149
24.12.1953
14 DAY INTERVALS
22.12.1954

FIG. 6

reduce the ability to move any distance. It is clear from an examination of Fig.6 p.92 that movement into dung is less during the colder seasons of the year.

Wolf (1938) found 28 to 30°C. lethal to <u>Lumbricus terrestris</u> while Rogers and Lewis (1914a) found the body temperature of <u>Lumbricus agricola</u> followed that of the environment (immersion in water) closely and rapidly. These authors (1914b) considered that the activity (contraction of the dorsal blood vessel) of this species was increased by an increasing temperature within the range 9.5 to 24.6°C.. Kim (1930) came to similar conclusions in his work with a species of the Megascolecidae. The extent of toleration to low temperatures is not known but -1°C. is not likely to prove lethal (Allee et als, 1949).

2. Activity related to Darkness and Rainfall

(i) Observations on the surface activity of Lumbricidae at night

Lumbricid activity of two distinct types was noted on the soil surface at night. While some worms retained their 'tails', several hind segments, within their burrows, others were entirely free of a burrow system. These types were collected separately on several nights until a hundred plus of each was obtained. The numbers of each species found at night entirely free on the surface and with their 'tails' in burrows are given in Table 28, p.95.

Discussion

At Moor House no appreciable Lumbricid activity was observed on the soil surface during daylight and none at night during frosty or dry conditions. The lowest temperature at which considerable activity was noted was 3.5°C. (Grass minimum reading).

Hogben and Kirk (1944) writing of *Lumbricus terrestris*, state :-

"Thus the earthworm is not equipped to emerge from its burrows except when the surface of

TABLE 28

LUMBRICIDAE FROM A COLLECTION AT THE SOIL SURFACE MADE AT NIGHT

Species	Free on surface		'Tail' retained in burrow	
	No.	%	No.	%
*L. terrestris	4	3.13	127	93.40
L. rubellus	46	35.94	5	3.68
L. festivus	16	12.50	1	.74
L. castaneus	21	16.41	0	0
D. rubida	16	12.50	0	0
Total pigmented species	103	80.48	133	97.82
+A. terrestris	3	2.34	3	2.21
A. caliginosa	15	11.71	0	0
O. cyaneum	4	3.13	0	0
E. rosea	3	2.34	0	0
Total unpigmented species	25	19.52	3	2.21
Total	128		136	

*Pigmented species

+Unpigmented species

the soil is exceptionally cool and moist"

Dreidax (1931) found only one species, Lumbricus terrestris, active at night and similarly this species was alone in a collection made at night in the U.S.A. but examined by Evans (1948b). This latter author, however, in the same paper states that three species of the 'tail in burrow' type are active at night at Harpenden, England, but does not name them.

Darwin (1881),after Morren (1829),refers to the habit of 'the earthworm' in retaining its 'tail'in its burrow when surface active at night and in pot experiments found worms very sensitive to vibrations, withdrawing immediately when so disturbed. Again by pot experiments, Darwin found that worms reacted only slowly to stimulation by light and would not emerge at all from pots kept artificially illuminated. The observations on the 'tail' in burrow type at Moor House agreed with Darwins findings.

Of the species given in Table 28,p.95, it seems that Lumbricus terrestris is practically unique in retaining its 'tail' in its burrow. Because of the extreme sensitivity to vibration of the 'tail' in burrow type, capture must be rapid and diagnosis of their behaviour visual and immediate. With the exception of Allolobophora terrestris this source of error is thought to account for the occasional records of other species found with their 'tails' in burrows. The numbers of A. terrestris in night collections were too small to allow an assessment of its behaviour on this evidence alone.

Of the Lumbricidae found 'free on the surface' several species are concerned which at least at the time of collection did not include an appreciable number of Lumbricus terrestris. Conclusions based on the numbers of the species in the collection are limited since the population of the area from which they were obtained is not accurately known. However, the population of a nearby area of similar soil type was estimated by soil sampling and is used for comparison. The totals of the pigmented and unpigmented group of species in the two collections are compared in Table 29,p.98.

TABLE 29

	Pigmented	Unpigmented	Total
Soil samples S.S.54	168	221	389
Free on the surface at night	103	25	128
Total	271	246	517

$\chi^2 = 53.02 \quad p. = .001$

It is clear that a high proportion of the Lumbricidae active at night belong to the pigmented group of species.

The number of mature and immature specimens of the pigmented and unpigmented groups of the night collection are compared in Table 30.

TABLE 30

	Pigmented Species	Unpigmented Species	Total
Mature forms	49	23	72
Immature forms	54	2	56
Total	103	25	128

$\chi^2 = 16.35 \quad p. = .001$

The proportion of mature specimens in the unpigmented group is significantly high. The analyses of Tables 29 and 30 suggest that surface activity at night is relatively uncommon in the unpigmented group of species and that when it does occur it is associated with their sexual condition.

(ii) <u>Activity measured by records from dung</u>.

Night activity was investigated by examining some of the sites discussed in Section III at less than 24 hour intervals. From the 8th. - 12th. June 1954, E.S.28 was examined at 0600, 1200, 1800 and 2400 hrs. B.S.T. and from the 15th - 21st September 1954, sites 27 - 30 were examined at 0600 and 1800hrs. B.S.T. The results of the examination of E.S.28 in 6 hour periods are given in Table 31,p.100, those for E.S.27 - 30 in 12 hour periods in Table 32,p.101.

The effect of rain on Lumbricid movement is assessed from the activity recorded in one of the replications of E.S.32 for the 15 days between the 2nd. - 16th. June 1954 and the result given in Table 33,p.102.

The amount of rainfall at Moor House was measured at the meteorological station by a daily continuous rain recorder and the number of hours rain for the relevant periods calculated from these records included in Tables 31 - 33.

TABLE 31

TOTAL LUMBRICIDAE AND HOURS OF RAIN IN 6 HOUR PERIODS

EXPERIMENTAL SITE 28

		0600 to 1200hrs	1200 to 1800hrs	1800 to 2400hrs	2400 to 0600hrs	Total
8 June	No. of worms	8	8	2	8	26
	Hours of rain	0	2.6	.4	0	3.0
9 June	No. of worms	5	13	6	5	29
	Hours of rain	3.4	1.0	.4	0	4.8
10 June	No. of worms	1	9	3	4	17
	Hours of rain	0	5.6	.4	0	6.0
11 June	No. of worms	4	4	6	2	16
	Hours of rain	2.0	0	1.6	1.6	5.2
12 June	No. of worms	7	3	2	2	14
	Hours of rain	0	.4	0	0	.4
Total No. worms		25	37	19	21	102
Total hours rain		5.4	9.6	2.8	1.6	19.4

TABLE 32

TOTAL LUMBRICIDAE AND HOURS OF RAIN IN 12 HOUR PERIODS

EXPERIMENTAL SITES 27 - 30

	Sites 27 and 28				Sites 29 and 30			
	18-0600hrs		06-1800hrs		18-0600hrs		06-1800hrs	
	No.of worms	Hours rain	No.of worms	Hours rain	No.of worms	Hours rain	No.of worms	Hours rain
15 Sept.	28	4.9	29	0	/	/	52	0
16 Sept	52	6.8	17	1.4	89	6.8	24	1.4
17 Sept	15	0.2	4	1.0	28	0.2	18	1.0
18 Sept	8	0	12	0	8	0	13	0
19 Sept	5	1.6	4	0.5	11	1.6	7	0.5
20 Sept	10	5.0	19	3.6	24	5.0	14	3.6
21 Sept	/	/	/	/	16	2.6	/	/
Total	118	18.5	85	6.5	176	16.2	128	6.5

TABLE 33

LUMBRICIDAE FROM THE DUNG OF ONE REPLICATION OF EXPERIMENTAL SITE 32 COMPARED TO HOURS OF RAIN - DAILY TOTALS

Dates of Examination June 1954	Hours of Rain	Number of worms
2	0	12
3	0	2
4	0	2
5	0	2
6	0	0
7	0	6
8	.4	3
9	3.4	36
10	5.0	48
11	6.8	39
12	6.8	15
13	.4	15
14	0	12
15	.4	0
16	15	60

The differences between the totals obtained in 6 hour periods (Table 31,p.100) are not significant and the dark period,24 - 0600hrs., did not produce the most worms. On the other hand the numbers found in the 12 hour periods (Table 32,p.101) are significantly different and greater for the dark period, 18 - 0600hrs.. This apparent contradiction is explained by the association of activity with the state of the ground as measured by the extent of rainfall. Thus, the numbers found in 24 hour periods (Table 33,p.102) are significantly different from each other and closely correlated with the number of hours of rain ($r = +.9033$, $z = 1.49$, $s = .289$). These daily totals of hours of rain and numbers of worms are contrasted in a histogram Fig.7,p.105. Similar histograms for the bulk totals of the less than 24 hour periods, Fig8,p.106, demonstrate the same correlation. Thus, there is increased activity during rainfall which is at least more important than any resulting from the effects of darkness.

It appears, therefore, that species of Lumbricidae found free on the surface at night may be equally active during daylight but remain concealed within the surface mat of vegetation. Hess (1924) working with Lumbricus terrestris states that this species is light sensitive, reacting negatively to all but the weakest illumination. This author (1925) also showed that the sub-epidermal pigment layer of Lumbricus terrestris acted as a shield to the photo-receptors so that their stimulation is through "pin-point windows" formed by nerve endings. Although no comparative work on the light sensitivity of Lumbricidae is known it could be assumed that Hess's conclusions applied equally to all pigmented species and that they, therefore, differ fundamentally from the unpigmented group. Thus, the pigmented Lumbricidae may be supposed to have a mechanism for controlling the extent of their exposure during surface movements necessary to their nomadic habits while the unpigmented have not.

FIG. 7.

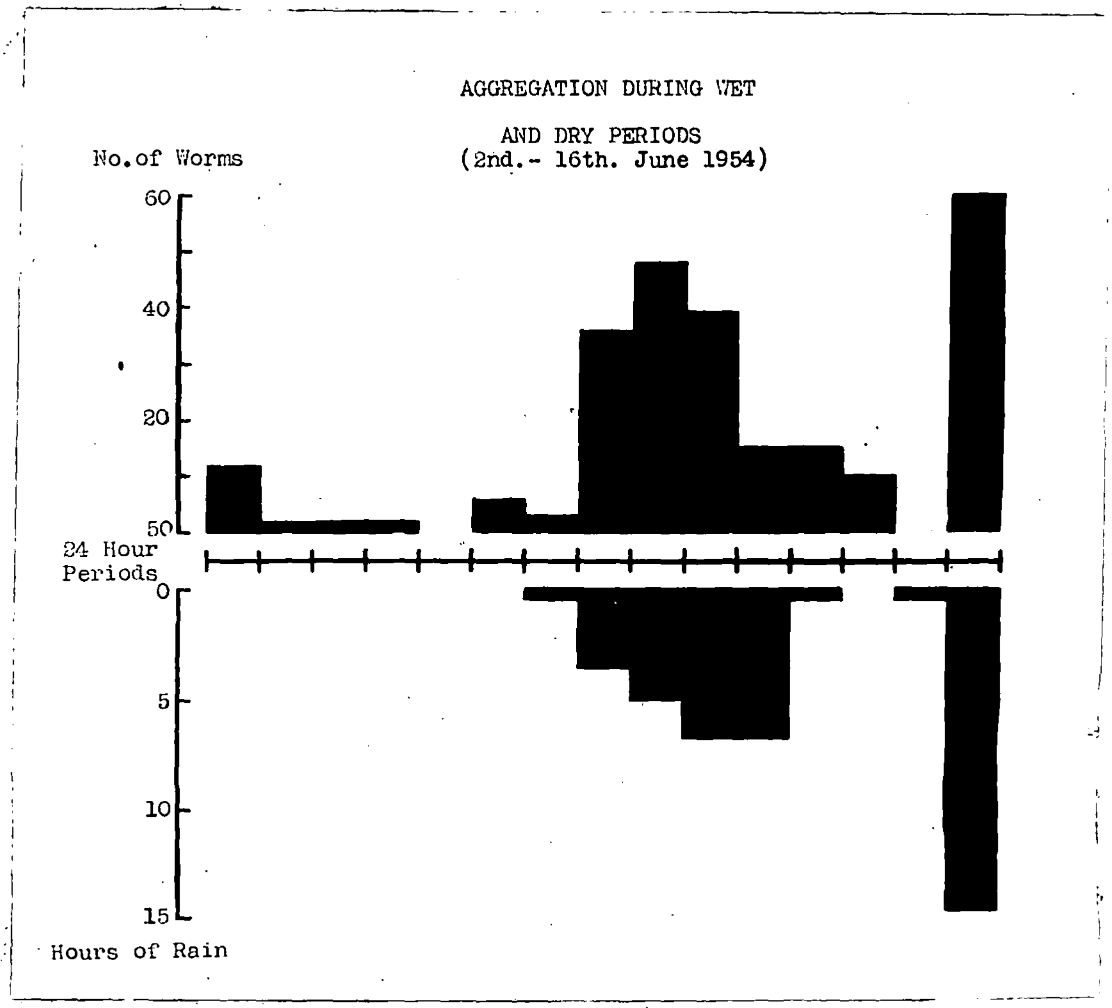
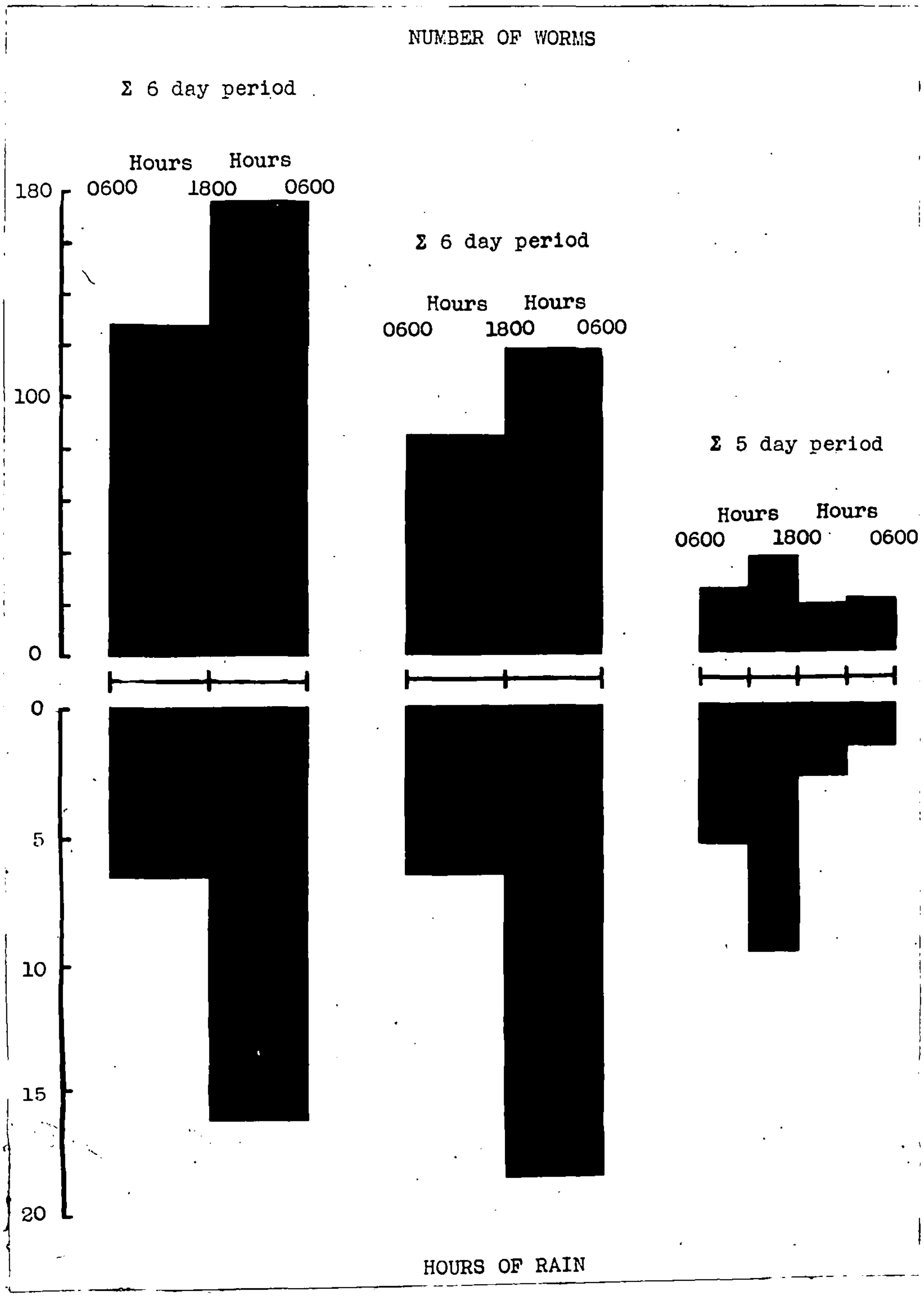

AGGREGATION DURING WET
AND DRY PERIODS
(2nd.- 16th. June 1954)
No. of Worms
60
40
20
50
24 Hour
Periods
0
5
10
15
Hours of Rain

FIG. 8.


NUMBER OF WORMS
Σ 6 day period
Hours
Hours
0600
1800
0600
Σ 6 day period
Hours
Hours
0600
1800
0600
Σ 5 day period
Hours
Hours
0600
1800
0600
180
100
0
0
5
10
15
20
HOURS OF RAIN

VI. Examination of gut contents.

Methods

Smears of the gut contents of several species of the pigmented and unpigmented groups were mounted in Canada balsam and examined with a petrological microscope.

The specimens examined had been preserved immediately on capture in 4% formalin.

The following species were examined :-

Of the pigmented group:-

Dendrobaena octaedra	19	specimens
" rubida	13	"
Lumbricus rubellus	25	"
Bimastus eiseni	13	"

Of the unpigmented group:-

Allolobophora chlorotica	36	specimens
" caliginosa	13	"
Octolasium cyaneum	11	"
" lacteum	3	"
Eisenia rosea	5	"

All smears were taken from the gut immediately behind the position of the clitellum.

Results

Three types of material were distinguished in the smears:-

1. Large, clearly recognisable portions of plant material.
2. Mineral material; demonstrable under crossed-Nicols.
3. Small particles of organic material.

Of these types of material the pigmented group contained 1 and 3 and very little 2 while the unpigmented species contained 2 and 3 and very occasionally 1.

Photographs of a smear from a representative of each group with and without crossed-Nicols are shown in Plates 6 - 9, pp. 109 - 110.

A quantitative estimate of the proportions of the type materials for each species was not made nor were the effects of the habitat from which the specimens were taken assessed. Nevertheless, it is apparent that wide differences can exist between the kind of food material eaten by different species.

PLATE 6.

Lumbricus rubellus

Smear of Gut Contents - Normal Transmitted Light.

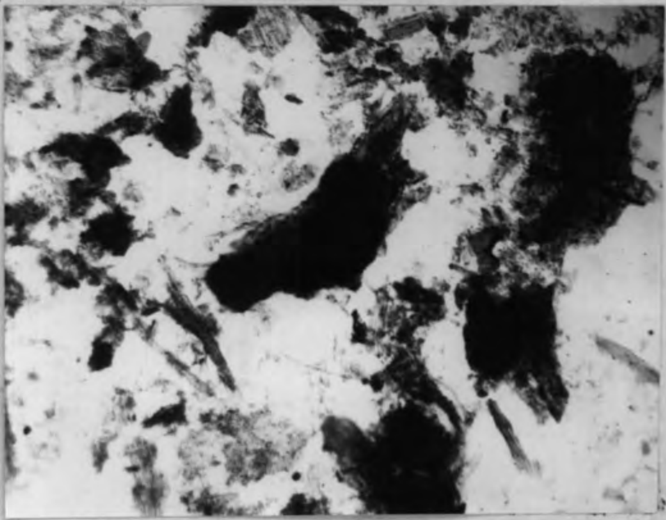


PLATE 7.

Octolasium cyaneum

Smear of Gut Contents - Normal Transmitted Light.

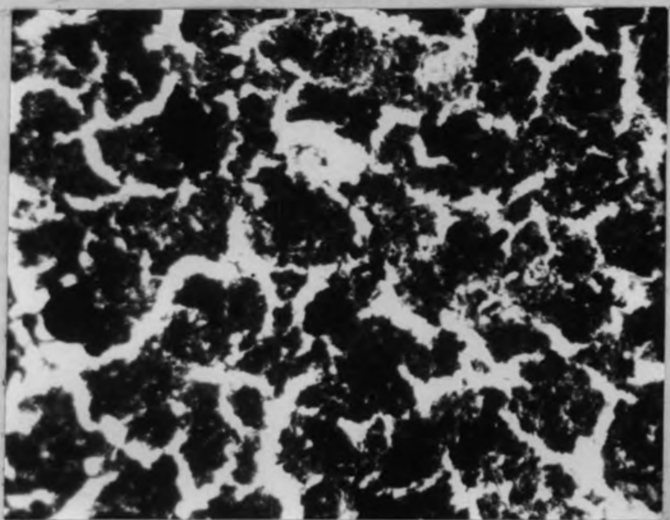


PLATE 8.

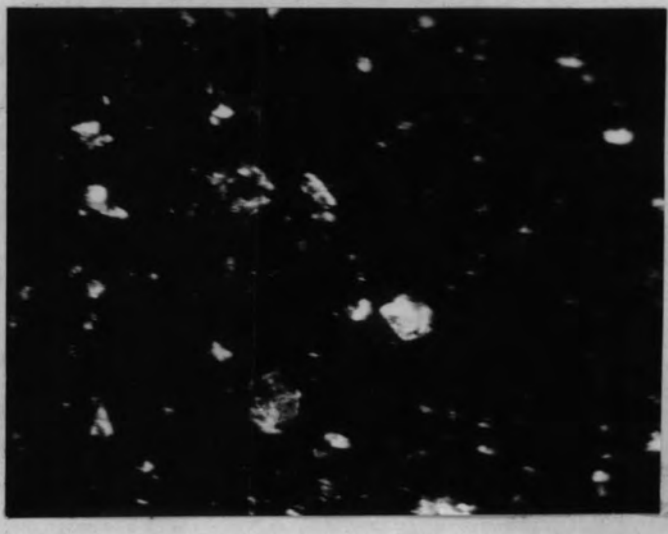
Lumbricus rubellus

Smear of Gut Contents - Light through crossed-Nicols.

PLATE 9.

Octolasium cyaneum

Smear of Gut Contents - Light through crossed-Nicols.



PART III

THE DISTRIBUTION OF THE LUMBRICIDAE AT MOOR HOUSE

Introduction

Müller (1889) demonstrated that different species of Lumbricidae are typical of different soil types and outstanding among others, Bornebusch (1930) confirmed and amplified his findings.

Guild (1948) showed differences between species complexes and their populations which were associated with the mechanical properties of soil types. The significance of agricultural treatments because of their effects on soil temperature and water content was demonstrated by Evans and Guild (1947b and 1948b). Krüger (1952) considered the mechanical effects of different agricultural treatments important but Tischler (per.comm.) now thinks his conclusions were premature and that the timing was more decisive than the treatment. In discussing the distribution of a Lumbricid population Guild (1951a) suggests soil acidity as a controlling factor while in 1952a this author also considered water content to be important. A positive correlation between population size and the calcium content of the soil was demonstrated by Nielson (1951). Conversely, Satchell (1955b) considered pH to be more important than calcium deficiency in controlling Lumbricid distribution.

The biological information deduced by these authors is based on the assumption that a species is found most frequently and at its highest population level, in its optimum habitat. Thus, a correlation between species distribution and habitat demonstrates some of the species requirements.

A species cannot, however, develop in an area that it cannot reach so the position is complicated by the ability of a species to cross barriers; the 'vagility' of Allee et als.(1949). Muldal (1952a) states that 201 of the 220 species of Lumbricidae are restricted in area and of local origin whereas only 19 are peregrine. This suggests that geographical barriers are of some importance to the group as does the observation of Evans and Guild (1947b) that Allolobophora nocturna Evans. was not found by Guild (1948) in Scotland. The importance of geographical range is perhaps of particular significance at Moor House where large differences in environment may occur as a result of the range in altitude.

The possible effects of interspecific competition should also be considered in assessing the value of correlations between habitats and species distribution. Michaelson (1903) suggested that among the other Oligochaete families of similar habit, only the genus Pheretima of the Megascolecidae could successfully compete with the Lumbricidae. Muldal (1952a) agreed with Michaelson and stated that the Lumbricidae often displace the indigenous 'earthworms' of other families on invading new territory. Thus, it seems possible that otherwise optimum habitats may be made unsuitable by the competition of another species.

Species lists of Lumbricidae from areas at all similar to Moor House are not common. Forrest et als.(1929-36) in a survey of the Isle of Barra found Lumbricus terrestris L. and rubellus Hoffmeister, Octolasium lacteum (Oerley), Eisenia rosea (Savigny), Bimastus eiseni (Levinsen) and tenuis (Eisen) and Eiseniella tetraedra f.typica (Savigny). Backlund(1951) at between 650 - 1,000 metres altitude (2,125 - 3,270ft.) in Swedish Lapland records *Dendrobaena octaedra*(Savigny) and *subrubicunda* (Eisen). Both *B.tenuis* and *D.subrubicunda* may be synonyms of *Dendrobaena rubida* (Savigny)(Graff,1953) and if this is accepted then all the species found in these two areas also occur at Moor House.

This part of the study distinguishes 'habitats' and while imperfect methods and small numbers of samples do not allow a complete survey, gives some estimates of their Lumbricid populations.

I. The habitats of Lumbricidae recognised at Moor House.

Pearsall (1950) reviewed the major soil and vegetation types of British upland and where possible some of the distinctions he made are used as 'habitats'. Thus, habitat is employed here simply as a recognisably distinct area of vegetation or soil type.

1. Limnic Habitats.

Parts of the stream beds are made up of raw alluvium which although very wet is never constantly and only rarely, completely immersed by the stream. Other limnic habitats occur where there is some form of spring providing a constant but shallow flow of water.

2. Peat Habitats.

The bulk of the reserve is covered with a deposit of peat with a characteristic vegetation complex of *Calluna*, *Eriophorum*, *Sphagnum* etc.. The peat is acid and anaerobic and for these reasons cannot be considered an optimum habitat for Lumbricidae. This area is distinguished as 'moor and bog' in the text but on occasion is subdivided into three types :-

Eriophorum moor (Pearsall,1950)	:	areas with large expanses of naked peat and some *Eriophorum* as the dominant but patchy vegetation.(Plate 10 p.117)
Blanket bog (Pearsall,1950)	:	areas with *Calluna*,*Eriophorum* etc. but characterised by an almost continuous *Sphagnum* cover. (Plate 11,p.118)
Calluna moor (Pearsall,1950)	:	drier area with *Calluna* and *Cladonia* and very little *Eriophorum* or *Sphagnum*.

A furthur peat habitat recognised, is the sum of many complex divisions intermediate between the deep peat of moor and bog and the mineral soils. This is distinguished as 'moor edge' and is characterised by the growth of *Juncus*, *Carex* and *Polytrichum* species. (Plate 12,p.119) The term 'moor edge' is used since these areas often divide the 'moor and bog' from the grass of mineral soils or the free water of a base-rich flush.

PLATE 10.

'ERIOPHORUM MOOR'

PLATE 11.

'BLANKET BOG'

PLATE 12.

'MOOR EDGE'

3. Mineral soil habitats.

(i) Drift

Mineral soils are primarily derived from the weathering of underlying rock material and may, therefore, be sometimes characterised by the parent rock. At Moor House the weathered material or 'drift' is so mixed that none of the soils can be said to have arisen from one rock type alone (Johnson per.comm.). The drift originally covered most if not all the area and may be seen underlying the peat in profiles cut by stream action etc.. Two habitats derived from exposed drift are recognised.

'Without raw humus'

Some of the drift overlying limestone is affected by the base-rich rock, producing a clayey soil with a mixed fauna and flora (See Plate 3,p.65) and a humus of the mull type. (Pearsall,1950) It is characterised by its rich flora and lack of raw humus in the soil profile.

'Sandstone grassland'

On some of the higher areas the drift has been exposed and carries a typical grassland of Festuca and or Nardus species developed on weathered sandstone (Park, per.comm.). This soil, however, has a podsol profile and the humus is of the mor type (Pearsall, 1950).

A furthur mor type 'habitat' is *Nardus* grassland (Pearsall, 1950), it may be derived from either drift or peat and is characteristic of some fell slopes, e.g. the North East slope of Knock Fell.

(ii) Alluvium

Many streams dissect the reserve and these invariably have banks of an alluvial deposit derived from the drift and peat. They exhibit a wide range of soil types dependent on the different proportions of these constituents. Areas of this type are summed by Pearsall (1950) as alluvial grassland but are here separated into four types recognised by their appearance :-

'Without raw humus'; a brown soil of fine texture. This habitat is not distinguished from the soils overlying limestone outcrops from which it is largely formed or influenced.

'Redeposited peat'; a black soil with a low mineral content.

'Coarse alluvium'; a grey, gritty soil from which the fine clay particles have been removed by stream action (Johnson, per.comm.).

'Mixed alluvium'; intermediate soils which cannot be readily assigned to any of the other types.

Samples of soil from between 3-6cm. were taken from 53 sites over the range of soils (The 1952 soil sites,p.131) on the same day and their water content and loss on ignition measured. The samples were dried to a constant weight at 105°C. to measure their water content and ignited at 600°C. to give their loss on ignition.

The results of examination of the 53 soil samples are given in detail in Appendix 8. As an example of the difference between the extremes of the range the percentage of the dry weight lost on ignition for those samples from the 'without raw humus' and 'redeposited peat' sites are compared in Table 34, p.123.

TABLE 34

SOIL - PERCENTAGE DRY WEIGHT LOST ON IGNITION AT 600°C.

'Without raw humus'		'Redeposited peat'	
Site No.	% loss on ignition	Site No.	% loss on ignition
15	14.15	4	47.82
38	24.42	9	29.27
39	13.87	11	30.50
44	18.17	12	43.38
48	14.07	13	50.49
49	12.00	14	35.51
52	29.72	20	33.03
54	19.88	22	33.17
		23	31.31
		26	75.46
		27	68.55
		50	33.42

II Quantitative aspects of the distribution of Lumbricidae at Moor House.

1. Population estimates from soil samples.

(i) Sample size

Habitats were examined by the soil sampling methods discussed in Part I,p.22. The two samplers used are distinguished by the surface area of the samples cut as either 1/25th. or 1/35th. of a square metre.

Underestimates can be expected of the deep living species, Allolobophora terrestris f.longa and Lumbricus terrestris (Evans and Guild, 1947b) which, however, only occur rarely in the area studied. Octolasium cyaneum on the other hand is common and may also be underestimated because of deep burrowing habits. With the possible exception of these species it is thought that the bulk of the Lumbricid population is found within the sample depth of 20cm. (Bornebusch, 1930)

The number of samples necessary for an accurate estimation of a population of any area is dependent on the sample size and the distribution of the population. There is a statistically ideal sample size in terms of the number of animals expected per sample but in sampling Lumbricidae it is impracticable. Thus, any samples smaller than the 1/35th.sq.m. used would damage too many specimens, rendering identification impossible. Table 35 gives a comparison of the proportions of damaged and undamaged specimens obtained from groups of samples of the two sizes used.

TABLE 35

	Damaged specimens	Undamaged specimens	Total
Six samples of 1/35th.sq.m. ex S.S.43, 1954.	27	77	104
Five samples of 1/25th.sq.m. ex S.S.43, 1952.	7	98	105
Total	34	175	209

$\chi^2 = 14 \quad p. = .001.$

Clearly there is a greater proportion of damaged specimens extracted by the samples of smaller size.

(ii) Aggregation shown by a comparison of adjacent samples.

As a guide to the possible extent of aggregation in the populations, two sites (Soil sites 43 and 54) of 1 square metre were sampled completely by taking 25 adjacent soil samples. The relative position of each sample was recorded (Appendix 9) and the number of each species per sample is given in Appendix 10 (S.S.43) and 11 (S.S.54).

Since the samples were adjacent the totals by species given in Table 36,p.127 are an accurate representation, in each case, of the population of 1 square metre to a depth of 20cm.

To demonstrate aggregation, the numbers per species per sample may be arranged in the spatial pattern in which they were found and their totals by blocks of five samples, horizontally and vertically, compared by χ^2. The distribution of *Octolasium cyaneum* found in Site 54 is given in Table 37,p.128 as an example of this treatment.

<u>TABLE 36</u>

<u>TOTALS BY SPECIES FROM THE 25 SAMPLES</u>

<u>OF SOIL SITES 43 AND 54</u>

Species	'Mixed alluvium' Soil site 43	'Without raw humus' Soil site 54
L. rubellus	49	79
L. festivus	2	64
L. terrestris	0	1
D. rubida	14	24
Total*	65	168
O. cyaneum	28	83
A. chlorotica	241	6
A. caliginosa	54	93
A. terrestris	0	38
E. rosea	81	1
E. tetraedra	1	0
Total+	405	221
Grand Total	470	389
Pigmented Group total weight	8.488g.	28.466g.
Unpigmented Group total weight	43.573g.	81.436g.
Total weight	52.061g.	109.902g.

+ Unpigmented group * Pigmented group

TABLE 37.

THE DISTRIBUTION OF O.cyaneum IN SOIL SITE 54.

					Totals	
2	0	1	2	0	5	
2	0	2	1	2	7	Horizontal
7	2	1	6	4	20	block X^2 = 23.93
8	5	4	6	3	26	p. = .001
3	11	2	3	6	25	
Totals 22	18	10	18	15	83	

Vertical block X^2 = 4.77, p. = .30

The results by X^2 of a similar treatment for all the species in both sites are given in Table 38,p.129.

Only Allolobophora chlorotica in Site 43 occurred in sufficient numbers for it to be analysed by X^2 as though the 25 samples had been randomised. The result is to disguise the aggregation giving a X^2 of 31.93,p. = .15.

Satchell (1955b) showed aggregation in several species and considered it to be a result of delayed spread following rapid reproduction. An examination of Allolobophora chlorotica from

TABLE 38

RESULTS OF A COMPARISON BY χ^2 - DISTRIBUTION OF THE MORE NUMEROUS SPECIES IN SOIL SITES 43 AND 54

	Soil site 43		Soil site 54	
	Horizontal blocks	Vertical blocks	Horizontal blocks	Vertical blocks
L.rubellus	36.81*	14.57*	7.01	4.35
L.festivus	/	/	1.78	7.56
O.cyaneum	19.50*	3.07	23.93*	4.77
A.chlorotica	3.89	17.15*	/	/
A.caliginosa	3.78	6.19	11.05*	2.12
A.terrestris	/	/	2.26	5.16
E.rosea	1.16	2.02	/	/

* p = .05 or less.

Site 43 does not support this view since the aggregation appears to be due entirely to the mature individuals. The horizontal and vertical blocks of the two groups are shown in Table 39 with the results of their analysis by X^2.

TABLE 39.

	MATURE SPECIMENS		IMMATURE SPECIMENS	
	Horizontal blocks	Vertical blocks	Horizontal blocks	Vertical blocks
Σ 1.	14	36	43	37
Σ 2.	14	15	37	25
Σ 3.	18	14	22	33
Σ 4.	19	6	27	31
Σ 5.	16	10	31	34
X^2 =	1.28	33.38	8.5	2.5
p. =	.85	.001	.07	.60

Active movement into dung has been demonstrated for the pigmented group of species and in the unpigmented group high proportions of mature/immature specimens were active at night and also aggregated near dung. It seems therefore, as if aggregations of Lumbricidae could occur as a result of slower movement through more favourable localities (Allee et als.,1949).

(iii) <u>The range in populations in alluvial soils</u>.

Fifty three sites were chosen, on the mineral soils, along the length of the banks of the three streams, Netherhearth Syke, Rough Syke, and Moss Burn and in the summer of 1952 two samples of 1/25th.sq.m. taken from each. (See map, Appendix 4 and description, Appendix 5)

In all cases worms removed from samples by hand sorting were preserved in 4% formalin, identified where possible and then weighed. Before weighing the preserved specimens were dipped in 95% alcohol and the surface film removed by filter paper.

The results by species for the sites of four 'habitats' are given :-

'Without raw humus'	Table 40, p.132
'Redeposited peat'	Table 41, p.133
'Coarse alluvium'	Table 42, p.134
'Mixed alluvium'	Table 43, p.135

TABLE 40

TOTALS BY SPECIES FROM TWO 1/25TH.SQ.M.SAMPLES OF 'WITHOUT RAW HUMUS' SOILS

Species	Soil site numbers				Soil site numbers			
	15	38	39	44	48	49	52	54
L.festivus				5		2	2	6
L.rubellus	1	2		15	4	3	4	3
D.rubida	1	1		1				1
D.octaedra				1				
Total*	2	3		22	4	5	6	10
O.cyaneum	8	3	4		5	3		7
A.chlorotica		13	13	5	1	15	17	1
A.caliginosa		8	12	16	5	2	15	5
A.terrestris							2	3
E.rosea		1		2		1	3	
Total+	8	25	29	23	11	21	37	16
Grand total	10	28	29	45	15	26	43	26
Total weight unpigmented group in g.	5.42	5.08	5.81	4.21	3.61	2.27	6.44	10.24

* Pigmented species

+ Unpigmented species

TABLE 41

TOTALS BY SPECIES FROM TWO 1/25TH.SQ.M.SAMPLES OF 'REDEPOSITED PEAT' SOILS

Species	4	9	11	12	13	14	20	22	23	26	27	50
		Soil site numbers					Soil site numbers					
L.rubellus		1	1		2	1	1		5			5
D.rubida		1		1			35	3	7	3		10
D.octaedra		1			1				3			
Total*		3	1	1	3	1	36	3	15	3		15
A.chlorotica							15	5	9			
E.rosea									2			
Total+							15	5	11			
Grand total		3	1	1	3	1	51	8	26	3		15
Total weight unpigmented group in g.							2.88	.54	1.24			

* Pigmented species + Unpigmented species

TABLE 42

TOTALS BY SPECIES FROM TWO 1/25TH.SQ.M.SAMPLES OF 'COARSE ALLUVIUM' SOILS

Species	Soil site numbers 3	7	8	28	51
L.rubellus	5	1	8		3
D.rubida			4	1	1
D.octaedra	1				2
Total*	6	1	12	1	6
O.cyaneum	1	7		4	1
A.chlorotica	6		27	22	4
E.rosea	2				
Total+	9	7	27	26	5
Grand total	15	8	39	27	11
Total weight unpigmented group in g.	1.67	4.69	4.48	7.01	.71

* Pigmented species + Unpigmented species

TABLE 43

TOTALS BY SPECIES FROM TWO 1/25TH.SQ.M. SAMPLES OF 'MIXED ALLUVIUM' SOILS

Species	Soil site numbers 1	2	6	10	16	17	Soil site numbers 18	19	21	24	25	Soil site numbers 29	30	31	32	33	Soil site numbers 34	35	36	37	40	Soil site numbers 41	42	43	45	46	47	53
L.festivus																		1										2
L.rubellus	2	1	1	3		1						1			4	1	1	2				5	1	4	7	4		10
D.rubida		1	3	1	1	4	1	6	1	1	1			2			4	1			7	4	2			1		1
D.octaedra				4					4						3													
Total *	2	2	4	8	1	5	1	6	5	1	1	1		2	7	1	5	4			7	9	3	4	7	5		13
O.cyaneum		2		8			2	5		2		4				4	5		2	1		1		6		4		2
O.lacteum	2					3			11		9		2															
A.chlorotica	6	8	1			8	22	18	15	24	1	19	29	29	14	13	16	19	12	12	47	4	3	18	16	31	10	9
A.caliginosa												6			3		3	3	11	11	10	11	9	10	21	10	4	9
A.terrestris																												1
E.rosea	22	2							5	1			1											5	8	10	15	
Total +	30	12	1	8		11	24	23	31	27	10	29	32	29	17	17	24	22	25	24	57	16	12	39	45	55	29	21
Grand total	32	14	5	16	1	16	25	29	36	28	11	30	32	31	24	18	29	26	25	24	64	25	15	43	52	60	29	34
Total weight unpigmented group in g.	4.28	2.25	4.36	3.86		1.86	3.67	9.93	3.51	4.68	1.64	4.53	3.89	4.45	2.62	2.33	5.28	3.02	3.87	2.49	7.03	2.13	.80	5.33	4.60	8.84	2.83	3.22

* Pigmented species + Unpigmented species

TABLE 44

TOTALS BY SPECIES FROM 1/35TH.SQ.M.SAMPLES 1954

Species	'Mixed Alluvium'				'Without raw humus'	'Moor edge' peat
	S.S.17 5 samples	S.S.18 5 samples	S.S.29 5 samples	S.S.43 6 samples	S.S.55 9 samples	S.S.56 11 samples
L.rubellus	2	5	6	5	5	4
L.festivus	1					
B.eiseni						4
D.octaedra	1	2	2	2	11	30
D.rubida	3	12		3	9	2
Total*	7	19	8	10	25	40
O.cyaneum		4	6	3	11	
O.lacteum	1					
A.chlorotica	25	93	29	82	67	
A.caliginosa			2	8		
E.rosea				1		
Total+	26	97	37	94	78	
Grand total	33	116	45	104	103	40◊

* Pigmented species   + Unpigmented species

◊ Of this total 34 were found in one sample.

Further soil cores but of 1/35th.sq.m. were taken in 1954 from four of the 'mixed alluvium' sites examined in 1952 and two new sites (S.S.55 and 56) were examined in this way at Green Hole, a limestone outcrop 1/2 mile S.E. of the house. The results by species are shown in Table 44,p.136 which also gives the number of samples and the 'habitat'. The specimens from these samples were not weighed.

Guild (1951a) suggested a population of 12.72 worms per square metre for 'natural hill pasture' in Scotland. This may be compared with the 470 per square metre of 'mixed alluvium' (S.S.43,p127) or the 389 per square metre of 'without raw humus' (S.S.54,p.127) suggesting that the populations of Moor House are particularly high. The difference, however, is thought to be a result of the sampling methods (Part I,pp.24 - 32) and indeed a total population as low as 12.5 per square metre would be rarely found by the method used.

The possible range in population per square metre of the four common unpigmented species is given in Table 45,p.138 compared with the actual numbers found in the 1 square metre of Sites 43 and 54.

TABLE 45.

	Maximum*	Minimum*	S.S.43	S.S.54
O.cyaneum	100	12.5	28	83
A.chlorotica	587.5	12.5	241	6
A.caliginosa	262.5	25	54	93
E.rosea	275	12.5	81	1

*Calculated from the maxima and minima shown in Tables 40 - 43,pp.132 - 135 multiplied by 12.5.

The minima quoted obviously reflect the size of sample but the 6 Allolobophora chlorotica and 1 Eisenia rosea of S.S.54 demonstrate that very low populations may exist. Again, the value of the possible maxima is difficult to assess but that they are not simply grossly magnified aggregates is shown by the high number of Allolobophora chlorotica in S.S.43.

The population of Octolasium cyaneum appears to have a smaller range than that of the other three species and if this is so it may be a result of its larger size. A comparison of the weights of some mature specimens of the four common unpigmented species is given in Table 46,p.139.

TABLE 46.

	No. of specimens weighed	Total weight	Mean weight
O.cyaneum	16	21.378g.	1.134g.
A.chlorotica	121	26.036g.	.215g.
A.caliginosa	20	6.017g.	.304g.
E.rosea	9	1.600g.	.178g.

Bornebusch (1930) states :- "the total weight of animals in deciduous forest soil gradually falls in proportion to the deterioration in soil quality." This suggestion cannot be applied to the present detailed data because of the small numbers of samples. Table 47,p.140, however, shows the mean number of species, mean total and mean weight per site, of the unpigmented species in the four soil types distinguished.

TABLE 47.

Soil type	No. of sites	Mean No. of species	Mean total of worms*	Mean total weight*
'Redeposited peat'	12	.3	2.41	.3878g.
'Coarse alluvium	5	1.8	14.8	3.7098g.
'Mixed alluvium'	28	2.43	23.93	3.6868g.
'Without raw humus'	8	3.13	21.25	5.3866g.

*per 2/25th. of a square metre.

The difference between the unproductive 'redeposited peat ' and the productive 'without raw humus' is clear agreeing with the suggestion of Bornebusch (1930). For intermediate conditions the position is not clear but it is thought that there is a trend to greater weight in the better soils which is not necessarily shown by increased totals of worms. Thus, in site 43, 405 unpigmented specimens weighed 43.573g. and in site 54, 221 unpigmented worms weighed 81.436g.. Therefore, in the 'without raw humus' of site 54 just over half the number of individuals weighed nearly twice as much as the total for the 'mixed alluvium' of site 43.

This results from the presence of the larger species *Octolasium cyaneum* and *Allolobophora terrestris f.longa* in site 54 and exposes the weakness of judging the productivity of soils by the numbers of a group as variable as the Lumbricidae. Even if it is assumed that different species have similar requirements equal numbers cannot be considered of identical rank in their effects on the soil.

2. Population estimates from dung samples.

(i) Relative population estimates from searches for naturally disposed dung.

Certain areas were searched for sheep dung and its contained Lumbricidae, these are designated as search areas, S.A., and are shown on the map in Appendix 4 and described in Appendix 6. In every case the numbers of Lumbricidae in each piece of dung was recorded although separation to species was limited to the total for any one area. Fifteen areas of unknown size were searched in 1952 and were divided only as 'moor and bog' or 'alluvium'. The searches on mineral soils were made along the length of the banks of Netherhearth Syke in one day and were separated into the parts between the soil sites already marked.

In August 1953 four areas of relatively homogeneous vegetation and in 1954 one, were examined and some attempt made to estimate the area searched. This was not successful since difficulty was experienced in staying on the vegetation type chosen and the estimate of area was subjective.

The number of pieces of dung, those with Lumbricidae and the species found are listed; for the search of the alluvial habitat of Netherhearth Syke in Table 48,p.144 and for the remaining areas in Table 49,p.145.

A comparison of the proportions of invaded dung found above and below 2,000ft.(612m.) in the search of Netherhearth Syke (Table 48,p.144) is given in Table 50.

TABLE 50.

	Above 2,000ft (612m)	Below 2,000ft (612m)	Total
Pieces of dung without worms	39	13	52
Pieces of dung with worms	17	25	42
Total	56	38	94

$\chi^2 = 11.40 \quad p. = .001$

It is apparent that a greater proportion of the dung was invaded in the area below 2,000ft,(612m) than above that height. This is thought to be a reflection of the greater area of better soils below 2,000ft.(612m.) rather than a direct effect of altitude.

TABLE 48

SEARCH FOR DUNG ALONG THE LENGTH OF NETHERHEARTH SYKE

Species	Search areas			Search areas				Search areas		
	10*	11*	12*	13*	14*	15	16	17	18	19
Total dung with worms	5	2	4	2	4	4	2	7	4	8
Total dung	13	8	13	8	14	5	4	11	8	10
L.rubellus	2	1		1	2	2	3	2	3	
D.rubida	1					5		1	3	19
D.octaedra	2		2	1	3			4	2	2
B.eiseni	1	1	2			1		4	2	2
Total	6	2	4	2	5	8	3	11	10	23

*Above 2,000ft. (612m.)

TABLE 49

PIECES OF DUNG AND THEIR CONTAINED LUMBRICIDAE

FROM SEARCH AREAS

Search area	'Habitat'	Pieces of dung Total	Pieces of dung with worms	Lumbricidae L. rub.	Lumbricidae D. rub.	Lumbricidae D. oct.	Lumbricidae B. eis.	Total worms
7	Eriophorum moor	17	1			1		1
1	'Moor and bog'	36	9			2	8	10
2	'Moor and bog'	33	8			4	6	10
4	'Moor and bog'	44	22			47	24	71
8	'Moor and bog'	19	2	1			2	3
5	Calluna moor	50	14			22	23	45
6	Calluna	16	5			2	7	9
3	Sandstone grassland	66	15	2		13	9	24
20	Sandstone grassland	37	11*			4		4
9	Alluvial grassland	24	17	14	21	29	5	69

*Includes pieces with oöthecae.

The results of 'habitat' searches (Table 49 p.145) show large differences in the proportions of dung invaded both between the 'alluvium' and 'moor and bog' and within the latter itself.

The differences within the 'moor and bog' environment were further investigated by a quantitative search (S.A.21) in September 1954. A 25 metre line was laid and walked with a 2 metres stick held at right angles to the direction of the line. Twenty five randomised samples on each of three 'habitats' were taken in this way and since each sample was of 50 square metres, 1,250 of each 'habitat' were covered.

The vegetation types separated were :-

'Eriophorum moor' ; areas of nearly naked peat with some Eriophorum.

'Blanket bog' ; areas with a complex cover of Calluna, Eriophorum and Sphagnum.

'Calluna moor' ; drier areas with Calluna and Cladonia and very little Eriophorum or Sphagnum.

In each sample the number of pieces of dung found and the number of worms per piece was recorded. (See Appendix 12) Separation of the worms by species was limited to the totals for each 'habitat' and these with the totals of the dung found are given in Table 51, p.147.

TABLE 51

SEARCH AREA 21 - DUNG OF 1,250 SQUARE METRES EACH OF THREE TYPES OF MOOR

	Eriophorum moor	Blanket bog	Calluna moor	Total
Dung without worms	96	99	216	411
Dung with worms	8	27	84	119
Total dung	104	126	300	530
D. octaedra	3	29	58	90
B. eiseni	7	20	77	104
Total worms	10	49	135	194

No difference was observed between the proportions of the species concerned, _Dendrobaena octaedra_ and _Bimastus eiseni_, and they are therefore considered together in the following analysis.

Each of the 1,250 square metre areas differed in the total number of pieces of dung found. Naked peat with some _Eriophorum_, 104; _Calluna_, _Eriophorum_ and _Sphagnum_ complex, 126 and _Calluna_ with _Cladonia_ 300pieces. These totals are significantly different with a χ^2 of 130.52,p. = .001. Two sources of error may influence the results of a search of this kind, first the dung may be missed and secondly the age is unknown so that the length of time for which the dung has been liable to invasion cannot be assessed. The probability of finding the dung is greater with decreased vegetation and the age of the dung will tend to be greater in areas of low population (p.151). In terms of total available dung, therefore, these errors would, if operative, minimise the differences observed. Thus, there is more dung available to the Lumbricidae of the drier _Calluna_ dominant areas and less to those of the naked peat.

The proportion of invaded dung differs between the areas, being 7.69%, 21.43% and 28% respectively. Analysis of these proportions in a contingency table, Table 52, shows them to be significantly different.

TABLE 52.

	Eriophorum	*Sphagnum*	*Calluna*	Total
Dung with worms	8	27	84	119
Dung without worms	96	99	216	411
Total	104	126	300	530

$\chi^2 = 18.39 \quad p. = .001$

Thus, the number of Lumbricidae invading dung on naked peat is less than that on *Calluna* dominant areas. The total amount of dung found in any area is not a true measure of that which is available to the Lumbricidae. A total of 194 worms were found by 119 pieces of dung over the area as a whole, that is 1.63 worms per piece and the expected totals based on this mean are compared with the observed in Table 53.

TABLE 53.

	Eriophorum	Sphagnum	Calluna	Total
Observed	10	49	135	194
Expected	13.05	44.02	136.93	194
χ^2	.71	.57	.03	1.31
				p. = .50

Thus, measured only by the dung invaded, the number of worms in each 'habitat' is as expected.

Judged by either the number of worms or the number of species, it is clear that 'moor and bog' is an environment at the extreme of the Lumbricid range and that only parts are suitable for the development of even its typical species, *Dendrobaena octaedra* and *Bimastus eiseni*.

(ii) Low relative population estimates from examination of artificially disposed dung.

Experimental sites 3 - 16 (Part II, p.52) were of similar type and with the exception of 12 - 14 and 16 are directly comparable. The excepted sites were on terrace grassland and their dung was removed so rapidly by the large population of worms that they were abandoned. The difference in population between peat 'habitats' and terrace grassland 'habitats' is too large to be efficiently measured by the same method. Thus, in two examinations E.S.16 yielded 211 worms and was abandoned at the third while 12 - 14 had had their dung largely eaten before the first examination. It is, therefore, necessary in the case of terrace grassland 'habitats' to examine the dung at more frequent intervals than would be worth while in those of peat.

Sites 3 - 11 and 15, where the population was low gave results which are shown in Table 54, p.152, summed for three habitats. In this case the 'moor and bog' has been subdivided into areas with a thick cover of vegetation dominated by Calluna and areas of sparse vegetation characterised by Eriophorum.

TABLE 54

LUMBRICIDAE FOUND IN THE DUNG OF EXPERIMENTAL SITES 3 - 11 AND 15

E.S.	'Habitat'	O. lact.	L. rub.	D. rub.	D. oct.	B. eis.	Total
3	Eriophorum moor				2	4	6
4	Eriophorum moor					4	4
6	Eriophorum moor		1				1
7	Eriophorum moor						
8	Eriophorum moor		1				1
5	Calluna moor				10	14	24
11	Calluna moor					17	17
9	'Moor edge'			8		13	21
10	'Moor edge'			56	26	3	85
15	'Moor edge'	1	47	10	15	2	75

The 'moor edge' habitat has all four species well represented and with an average per site of 60.3 has a higher population than that of either the _Calluna_ moor, 20.5 or the _Eriophorum_ moor, 2.4.

The two specimens of _Lumbricus rubellus_ recorded on _Eriophorum_ moor were the only worms found in two areas in more than two years. This species is not typical of even _Calluna_ moor and since both areas were located more than 100 metres from 'moor edge' these records suggest that _L. rubellus_ may travel long distances in an unsuitable habitat.

Experimental sites 19 - 24 were of the same type (Part II, p.52) as 3 - 16 but situated on the ridge of Knock Fell at altitudes 2,375 - 2,425ft. (726 - 742m.) and examined only twice. The results are given in Table 55, p.154 and show the same relative differences associated with 'habitat' as sites at lower altitudes. There are, however, differences between the low and high altitude results for apparently similar 'habitats'.

On a limestone outcrop (E.S.22 at 2,425ft., 742 m.) surrounded on all sides by peat all four of the common pigmented species were found, as they were on grassland at the head of Netherhearth Syke, (E.S.23 at 2,375ft., 726 m.) In both cases Dendrobaena octaedra formed over 50% of the total, a much higher proportion of this species than was found on grassland at lower altitudes. Compared to other areas where the proportion of Dendrobaena octaedra was high, the totals from Knock Fell were remarkably high suggesting that some factor in this environment allows a greater development of this species.

On Nardus dominated vegetation at the top of the North East slope of the ridge, (E.S.23 at 375ft., 726 m.) Allolobophora chlorotica and Eiseniella tetraedra f. typica and hercynia formed 26.6 and 15.82% of the total number of worms found. This high proportion of unpigmented species found in dung was unique in the examinations undertaken in this study. (Part II,p.79)

TABLE 55

LUMBRICIDAE FOUND IN THE DUNG OF

EXPERIMENTAL SITES 19 - 24

KNOCK FELL

E.S.	'Habitat'	E. tet.	A. chl.	L. fes.	L. rub.	D. rub.	D. oct.	B. eis.	Total
21	Eriophorum moor								
19	Sandstone grassland			1			35	15	51
20	Sandstone grassland						37		37
24	Nardus grassland	23	37		60	17	88	1	226
23	Alluvial grassland		1		97	80	227	2	407
22	Limestone outcrop				16	18	44	4	82

(iii) High relative population estimates from examination of artificially disposed dung.

In 1954 wide differences were observed between the totals and proportions of the species obtained from the six closely spaced sites, E.S.27-32 (Pt.II pp.67 - 72). Three 'habitats' were covered by these sites; E.S.30, 'Moor edge'; E.S.29, 'without raw humus' and the remainder, 'mixed alluvium'. Of the four 'mixed alluvium' sites the vegetation of E.S.27 differed at a glance from that of the other three, being rank and little grazed.

The totals of all species found by all 'treatments' in these sites are given in Table 56, p.157. These grand totals, however, were obtained from a series of slightly different treatments between sites (number and times of examination) and so for a direct comparison, Table 57,p.158, gives the number of each pigmented species found in the first period of examination.

TABLE 56

LUMBRICIDAE FOUND IN THE DUNG OF EXPERIMENTAL SITES 27 - 32

Species	Without raw humus	Mixed Alluvium		Mixed Alluvium		Moor edge
	E.S.29	E.S.27	E.S.28	E.S.31	E.S.32	E.S.30
L.festivus	13	5	5		8	
L.castaneus	66					
L.rubellus	593*	227*	363*	322	416*	129
D.rubida	281	151	63	151	202	111
D.octaedra	3	61	24	10	35	11
B.eiseni	1			1		19
Total ◊	957	444	455	484	661	270
A.caliginosa	15	9				
A.chlorotica	45	72	59	13	56	
A.terrestris	1		2			
O.cyaneum	1	1	3		1	
E.rosea	4	2			7	
E.tetraedra				1		
Total +	66	84	64	14	64	
Grand total	1,023	528	519	498	725	270

◊ Pigmented species + Unpigmented species
* Contains a proportion of the other *Lumbricus* species

TABLE 57

PIGMENTED SPECIES FOUND IN THE DUNG OF EXPERIMENTAL SITES 27 - 32 IN THE PERIOD 1 - 16 JUNE 1954

Species	Without raw humus	Mixed alluvium		Mixed alluvium		Moor edge
	E.S.29	E.S.27	E.S.28	E.S.31	E.S.32	E.S.30
L.festivus	4	4	3		1	
L.castaneus	35					
L.rubellus	247*	166*	190*	258	219*	52
D.rubida	152	115	34	117	137	53
D.octaedra	2	55	12	7	15	9
B.eiseni				1		13
Total	440	340	239	383	372	127

* Contains a proportion of the other Lumbricus species

The 'moor edge' site differs from the others in containing Bimastus eiseni and in having a low total. The 'without raw humus' site is also distinct with, Lumbricus castaneus and a high total. Of the 'mixed alluvium' sites, 31 and 32 are similar while 27 differs from them in having a high number of Dendrobaena octaedra and 28 in a low number of Dendrobaena rubida. Analysis of these differences by χ^2 gives the results shown in Table 58.

TABLE 58

Sites analysed	D.octaedra		D.rubida		L.rubellus	
	χ^2	p.	χ^2	p.	χ^2	p.
27:28:31:32	39.77	.001	61.91	.001		
28:31:32	2.89	.20				
27:31:32			2.41	.30		
31:32					3.02	.07

(iv) The proportions of the four common dung associated species in three major habitats.

As suggested, three major habitats of Lumbricidae may be distinguished at Moor House. The grassland of the alluvial terraces and limestone outcrops; the deep peat of the 'moor and bog' and an intermediate condition at the edge of the moor or where flushing occurs, 'moor edge'. A comparison of the proportions of the four common species found in the dung of these environments is given in Table 59.

TABLE 59.

	Terrace grassland	'Moor edge'	'Moor and bog'
Number of sites	15	6	15
Total No. of worms	2,784	670	417
% *L. rubellus*	57.06	28.35	.71
% *D. rubida*	35.43	38.81	.00
% *D. octaedra*	6.58	26.86	50.12
% *B. eiseni*	.93	5.98	49.17

These divisions of the environment may be further subdivided, nevertheless, at this level there are clear differences between the species proportions found on any one type. Dendrobaena octaedra and Bimastus eiseni form the bulk of the population of the 'moor and bog' and give way to Dendrobaena rubida and Lumbricus rubellus on the better soils.

(v) Absolute population estimates.

The absolute population of the pigmented species in the habitats studied was difficult to estimate. Where the population is high as on the terrace it may be measured by soil sampling, these species are, however, particularly liable to aggregate so that a great many samples would be necessary to give a significant average. Where the population is low as on 'moor and bog' the soil sampling method would be too laborious to give efficient results.

'Terrace grassland'

Both the soil samples (Tables 40 - 44, pp.132 - 136) and the experimental sites (Tables 57, p.158) taken on terrace grassland show that large differences between areas can occur. From these results and the examination of two square metre samples (S.S.43 and 54, Table 36,p.127) it appears that populations of 50 - 100 per square metre are not unusual.

'Moor edge'

The results of a series of soil samples taken from 'moor edge' peat (S.S.56, Table 44,p.136) suggest a population of 127 per square metre. However, this estimate is derived from a total of 40 worms found in eleven 1/35th.square metre samples of which one contained 34 worms while the other ten gave only 6 worms. Without the sample containing 34 worms the population is estimated as 21 worms per square metre.

Areas of 4 square metres were isolated and the population of Lumbricidae trapped in dung (E.S.34, Part II, Table 27,p.89). From those areas where the trapping was most complete 73 worms were found in 16 square metres, that is,4.5 per square metre.

'Moor and bog'

Fifty 1/25th.square metre samples from Calluna moor (E.S.2, Part II,p.37) yielded 1 worm and 1 oötheca of Dendrobaena octaedra suggesting a population of 1 per square metre. The same site, however, covered with 66 pieces of dung over 50 square metres produced 1,083 worms in two years.

Dung deposited on three isolated 4 square metre areas of _Calluna_ dominant moor (E.S.33, Part II Table 27,p.89) produced 6 worms, that is, .5 per square metre.

From the search of naturally disposed dung of three 1,250 square metre areas of 'moor and bog' (S.A.21, Table 51,p.147) 10 worms were found in '_Eriophorum_ moor'; 49 in 'blanket bog' and 135 in _Calluna_ moor. Assuming all the Lumbricidae of these areas to have been in the dung at the time of examination these results suggest populations of .008, .039 and .108 worms per square metre.

III A review species by species of the distribution of the Lumbricidae at Moor House.

The distribution of the Lumbricidae at Moor House is discussed below by species and in each case a comparison made with records in the literature.

Of the literature reviewed four authors refer to most of the species. The conclusions of these authors are based on a survey of; Wicken Fen, an area of fen in South East England (Pickford, 1926); a variety of woodlands in Denmark (Bornebusch, 1930); pastures on several soil types in South East Scotland (Guild,1951a) and woodlands in the Lake District, North West England (Satchell,1955b). The latter author as a result of experimental work (1955b) considered pH "a factor of prime importance in determining the limits of distribution of earthworm populations" and in this respect assesses species as "acid tolerant", "ubiquitous" or "acid intolerant."

Lumbricus castaneus. (Savigny)

Lumbricus castaneus was found at Moor House in only one place; by an examination of dung on experimental site 29 (Appendix 7). It was missed by soil samples from the same place (S.S.44, Appendix 5) and did not occur in exhaustive dung samples from nearby. The soil of this site is 'without raw humus' a rich area of the mull type but by no means obviously unique except apparently for the presence of this species.

The species is surface active (Part II) and common in alluvial pastures of the surrounding district. Therefore, it seems unlikely that L.castaneus has recently invaded the reserve and not yet become widespread.

Bornebusch (1930) and Pickford (1926) considered L.castaneus to be a species of mull soils. Guild (1951a) found it in acid soils and Satchell (1955b) assessed it as 'ubiquitous' in acid tolerance. The evidence of distribution in this species is therefore conflicting and the reason for its restricted distribution at Moor House is unknown.

Lumbricus terrestris. L.

Night searches near the house showed Lumbricus terrestris to be common in the deep mull soils. The species occured only once in soil samples but it may be underestimated by this method (Evans and Guild, 1947b). It does not move into dung and since the only area searched at night was near the house it is possible that L.terrestris is more widespread than the results suggest.

Evidence of soil type preference by L.terrestris is again conflicting; Bornebusch (1930) and Pickford (1926) assign it to mull soils while Guild (1951a) found it in acid soils and Satchell(1955b) considers it "ubiquitous" in acid tolerance. All authors, however, agree that L.terrestris is deep living, making burrows to a depth of 2 metres or more (Hensen, 1877). The mineral soils of Moor House are not deep, few will exceed 50cm., which may act as a limiting factor to the distribution of this species.

Allobophora terrestris f.longa.(Ude)

Allolobophora terrestris f.longa was found only in soil samples, apparently uncommon and restricted to the better soils. It is another deep living species and Pickford (1926), Bornebusch (1930), Guild (1951a) and Satchell (1955b) agree that it is intolerent of acid soils.

Lumbricus festivus (Savigny)

Lumbricus festivus should be found equally well by either soil or dung samples. It appears, at Moor House, to live in mull soils but was recorded on one occasion on the mor soil of 'sandstone grassland'. Mull soils occur in the vicinity so that this record may have been a result of a nearby population.

Bornebusch (1930) and Guild (1951a) found this species sporadic in distribution and could not associate it with any particular soil type.

Allolobophora caliginosa (Savigny)

Allolobophora caliginosa is found only by soil samples and appears to be absent from the poorer soil 'coarse alluvium' and 'redeposited peat'. This is in agreement with the findings of Pickford (1926), Bornebusch (1930), Guild (1951a) and Satchell (1955b) who all consider it intolerant of acid conditions.

Counting only those habitats, 'without raw humus' and 'mixed alluvium', *A. caliginosa* is found in 9 of the 11 sites alongside Moss Burn but in none of the 6 each of Rough or Netherhearth Sykes (See map in Appendix 4). The number of sites is not great but no other species shows this kind of association. This may reflect the sensitivity of the species to soil type implying that Moss Burn differs from the other two streams in some respect, it certainly flows through more limestone (Johnson per.comm.) and Nielson (1951) found the population size in this species to be positively correlated with the amount of calcium in the soil. This was not comparative, however, in that Nielson found the Lumbricid population practically monospecific in the area of New Zealand studied.

Octolasium cyaneum (Savigny)

Octolasium cyaneum is a common species at Moor House found by soil samples in all but the most peaty soils.

Bornebusch (1930) considered it as a 'humid mull' species and Satchell (1955b) classifies it as 'ubiquitous' in acid tolerance.

Allolobophora chlorotica (Savigny)

Allolobophora chlorotica is the most widespread of the unpigmented Lumbricidae of the area occurring in 41 of the 54 mineral soils examined including some of the 'redeposited peat' sites. The species may be displaced at the other end of the range in the better mull soils as is apparent in a quantitative study (Table 36,p.127).

Pickford (1926) found A.chlorotica living in acid conditions among the roots of sedge fen plants; Bornebusch (1930) found it in "very clayey soil" (therefore very wet?); Cernosvitov (1945) and Davies (1951) record it as truly limnic and Satchell (1955b) considered it to be intolerant of acid conditions.

A.chlorotica was found occasionally in a limnic habitat at Moor House and it is considered that its general distribution there is a result of the high rainfall.

Eisenia rosea mut. macedonica (Rosa)

Although not as common as A.chlorotica, Eisenia rosea mut.macedonica is similarly tolerant of soil type at Moor House.

Pickford (1926) records it in acid conditions at the roots of sedge fen plants, Bornebusch (1930) found it in clay and Satchell (1955b) considered it intolerant of acid conditions.

Pickford (1926) thought the extensive papillation in this form and Octolasium lacteum was indicative of the wet conditions in which they lived.

Bornebusch (1930) found the species frequently aestivating and this was also noted at Moor House. This may be another indiction of a demand by this species for a high water content in its soil (Evans and Guild, 1947b).

Octolasium lacteum. (Oerley)

Octolasium lacteum was recorded from only 5 of the mineral soil sites ('mixed alluvium') and from the dung of Experimental site 15, a 'moor edge' habitat.

Pickford (1926) recorded the species as limnic while Bornebusch (1930) found it uncommon but in mull conditions.

Eiseniella tetraedra f.typica (Savigny) and mut.hercynia (Michaelson)

Eiseniella tetraedra was found mainly

during unsystematic searches of stream beds and flushes which may be considered its typical habitat.

Stephenson (1930) calls it an amphibious species; Pickford (1926) classifies it as limnic; Bornebusch (1930) found it in swamps and Guild (1951b) found it in flushes.

It does, however, occur away from free water and was found with A.chlorotica in dung on the Nardus covered slope of Knock Fell (E.S.24, Appendix 7). Guild (1951a) also records it away from free water, on a slope in 'rough pasture'.

Lumbricus rubellus. Hoffmeister

Lumbricus rubellus is the most common pigmented species at Moor House occurring in both soil and dung samples in all habitats but the peat of 'moor and bog'. In common with the following three it is a surface active species which compared to the unpigmented species, may be relatively independent of soil type. That this is not entirely so is suggested by its virtual absence from the 'moor and bog' sites (p.160).

Pickford (1926), Bornebusch (1930) and

Guild (1951a) found it widespread in all but the most acid conditions; Satchell (1955b) considered it "ubiquitous" in acid tolerance and as living in the surface litter of acid soils and burrowing only in mull soils.

Dendrobaena rubida. (Savigny)

Dendrobaena rubida at Moor House has a similar distribution to Lumbricus rubellus and they are usually found together.

Pickford (1926) found it sporadic but absent from fen peat; Bornebusch (1930) recorded it in compost heaps etc. (Syn.subrubicunda ?); Guild (1948) and Satchell (1955b) consider it tolerant to acid conditions.

Dendrobaena octaedra. (Savigny)

This species was found occasionally on all soil types but was typical of the most acid conditions, the peat of 'moor and bog'.

Ribacourt and Combault (1907) record D.octaedra as living in moss on high mountains; Bornebusch (1930) calls it "the most frugal of all

European species"; Drift (1951) found it in undecomposed Beech litter and both Guild (1948) and Satchell (1955b) consider it to be acid tolerant.

Bimastus eiseni. (Levinsen)

Bimastus eiseni has a similar distribution to that of *D.octaedra* but is even more restricted to the very acid organic soils of 'moor and bog'.

Bornebusch (1930) considered *B.eiseni* very rare and found it in the stubs of rotting trees etc.; Cernosvitov (1945) mentions Tetry (1938) as considering it common in caves and mines and himself records it as limnic; Guild (1938) and Satchell (1955b) both found it tolerant of acid conditions.

PART IV

GENERAL DISCUSSION

Systematics

Three infraspecific categories, forma, variety and mutatio are widely used in the separation of Lumbricid species. Evidence of the relative value of these distinctions is obscure and there appears to be little justification for their retention. Those forms which are known as distinct geographical races (e.g. possibly *Allolobophora terrestris* forma *longa* (Ude)) might be awarded subspecific rank, others, for which evidence is lacking, remaining with the one query, 'variety'. Within the species it is essential that all stages should be identifiable. There are, however, few descriptions of the immature forms available and these are widely scattered throughout the literature. Again, descriptions of oöthecae are known only from those of Evans and Guild (1947a) and they are incomplete even for the species involved. Muldal (1952a) has shown the importance of parthenogenetic reproduction to some species of British Lumbricidae. The possible effects of this factor, in assisting the spread of a species through the ability to reproduce freely in populations of low density, have yet to be investigated.

Form and function

The presence or absence of pigment is the only morphological difference used in this study to support observed differences of habit between Lumbricid species. Thus, it is assumed that the function of the pigment in controlling the light sensitivity of *Lumbricus terrestris* L. (Hess 1924 and 1925) is similar in all pigmented species (p.104). Few other morphological differences unconnected with the gonads are known and these such as prostomium shape, setae position etc. are of unknown function. It is unfortunate, in this respect, that experimentalists have restricted themselves to an examination of only one species at a time and this invariably either *Lumbricus terrestris* L. or *Eisenia foetida* (Savigny)(pp.3-4). Again, the artificial nature of many of these experiments makes it difficult to assess their results in terms of natural conditions.

Ecology

There are considerable divergences of opinion among authors who have suggested associations between soil type and Lumbricid species. These views are conflicting only when it is assumed that some factor determining soil type determines Lumbricid distribution. This, however, may not be true of all species or indeed, since there is little knowledge of their biology, of any. The possible independence of soil type of some species is supported by an examination of the distribution of _Dendrobaena octaedra_ (Savigny) and _Bimastus eiseni_ (Levinsen). These two species are 'widespread but local' throughout Europe and the one common factor of their varied habitats appears to be the unsuitability of these for other Lumbricidae. At Moor House _D.octaedra_ and _B.eiseni_, in that they are the only species present, are typical of 'moor and bog'. _D.octaedra_, however, attains greater numbers on mull soils at high altitudes (2,425ft.,742m.,p.155) where other Lumbricids are restricted and disappears (p.158) when other species are numerous. _B.eiseni_ was not abundant away from peat soils but within them decreased in numbers in the presence of species other than D. octaedra (pp.145,152 and 155).

As a group of soil living animals the Lumbricidae are of special interest because of their supposed effects on top-soil formation and maintenance (Cromptom,1953). These, however, cannot be investigated quantitatively until more is known of the comparitive biology of Lumbricid species.

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APPENDIX 1

The registration numbers of specimens of the Moor House Lumbricidae stored at the British Museum

Lumbricus castaneus (Savigny)	1955:5:10:56-60
" *festivus* (Savigny)	1955:5:10:61-65
" *rubellus* Hoffmeister	1955:5:10:66-70
" *terrestris* L.	1955:5:10:71-75
Allolobophora caliginosa f.typica (Savigny)	1955:5:10: 1- 4
" *chlorotica* (Savigny)	1955:5:10:31-35
" *terrestris f.longa* (Ude)	1955:5:10:26-30
Dendrobaena octaedra (Savigny)	1955:5:10:36-40
" *rubida* (Savigny)	1955:5:10:15-19
Octolasium cyaneum (Savigny)	1955:5:10:20-24
" *lacteum* (Oerley)	1955:5:10:10-14
Eisenia rosea mut.macedonica (Rosa)	1955:5:10:46-50
Eiseniella tetraedra f.typica (Savigny)	1955:5:10:41-45
mut.hercynia (Michaelson)	1955:5:10:51-55
Bimastus eiseni (Levinsen)	1955:5:10: 5- 9

Oöthecae

Dendrobaena rubida (Savigny)	1955:5:10:77
Bimastus eiseni (Levinsen)	1955:5:10:78
Dendrobaena octaedra (Savigny)	1955:5:10:79
Lumbricus rubellus Hoffmeister	1955:5:10:80

APPENDIX 2

THE NUMBER OF WORMS PER LOCUS EXTRACTED BY THE SOIL SAMPLING AND PERMANGANATE METHODS

Soil cores

Loci	L. terr.	L. cast.	O. cyan.	A. terr.	A. cal.	E. ros.	Total
1	7	12	1	10	11	14	55
2	11	12	2.5	25.5	11.5	26	88.5
3	8.5	9	1	20	8	15.0	61.5
4	11.5	10	0	26.5	8	15.5	71.5
5	9	9	2	24	7	10	61
6	8	4	4	21	14.5	6	57.5
7	10	4	.5	19.5	10	10	54
8	9	5	.5	19	15.5	15	64
9	10	7	1	21.5	19	10.5	69
10	9	6	2.5	27	6.5	6.5	57.5
Total	93	78	15	214	111	128.5	639.5
Av. per sq. m.	65.1	54.6	10.5	149.8	77.7	89.95	447.65

First permanganate treatment

Loci	L. terr.	L. cast.	O. cyan.	A. terr.	A. cal.	E. ros.	Total
1	6	4	0	21	5	0	36
2	7	0	0	11	2	1	21
3	10	8	0	23	9	7	57
4	7	2	0	13	3	1	26
5	1	5	0	20	1	1	28
6	3	1	0	19	6	0	29
7	3	3	0	21	8	1	36
8	7	2	0	28	7	2	46
9	5	4	0	22	5	1	37
10	1	3	2	20	6	2	34
Total	50	32	2	198	52	16	350
Av. per sq. m.	5	3.2	.2	19.8	5.2	1.6	35

Second permanganate treatment

Loci	L. terr.	L. cast.	O. cyan.	A. terr.	A. cal.	E. ros.	Total
1	2	3	1	3	6	1	16
2	7	0	0	9	6	9	31
3	19	4	0	7	8	10	48
4	7	1	0	14	1	1	24
5	8	7	0	9	0	1	25
6	6	2	1	5	7	0	21
7	8	2	0	4	3	3	20
8	12	6	1	12	7	6	44
9	15	0	0	9	5	4	33
10	7	3	2	11	7	2	32
Total	91	28	5	83	50	37	294
Av. per sq. m.	9.1	2.8	.5	8.3	5	3.7	29.4

APPENDIX 3

SOIL CORES - FIRST PERMANGANATE TREATMENT

Allolobophora terrestris f. longa

An example of the Analysis of Variance used to compare the species proportions found by the soil sampling and permanganate methods.

	% of species from 10 soil core loci	% of species from 10 first permanganate treatments	Total
1	a_1	b_1	t_1
.	.	.	.
.	.	.	.
10	a_{10}	b_{10}	t_{10}
Total	A	B	T

$$\text{Correction factor} = \frac{T^2}{20} = 41{,}570.79$$

$$\Sigma_1 = \frac{A^2 + B^2}{10} - \text{Correction factor} = 2{,}859.87$$

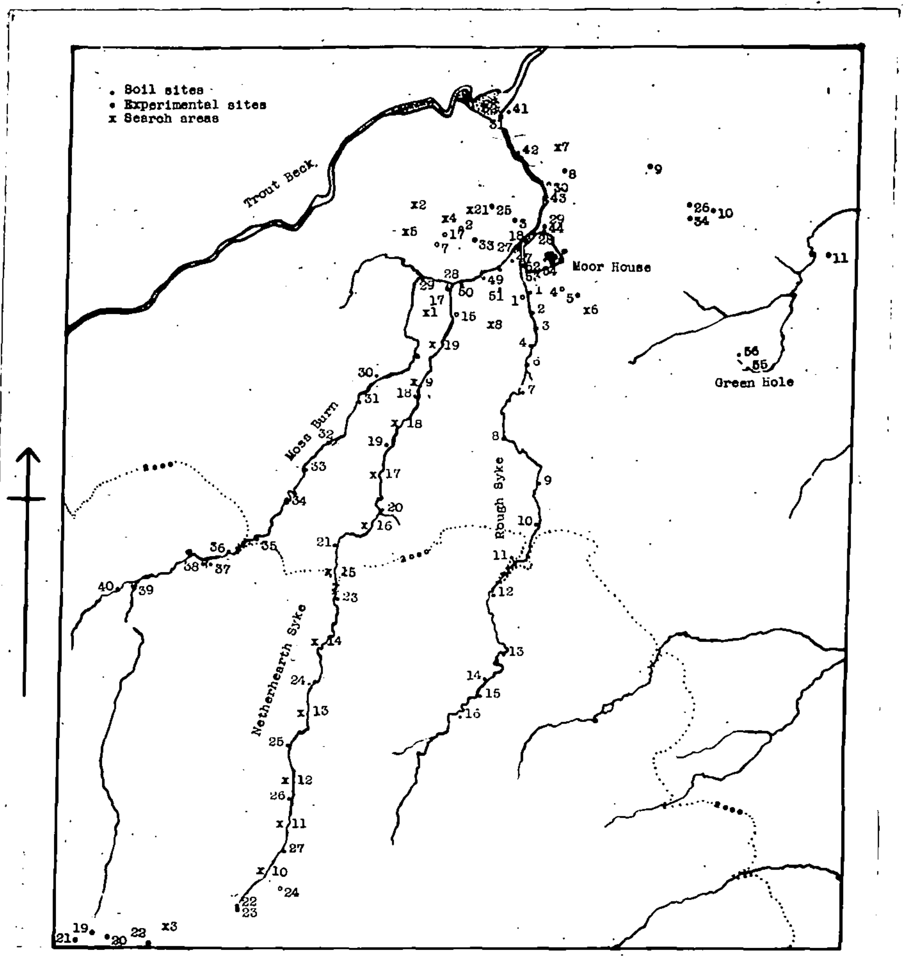
$$\Sigma_2 = \frac{t_1^2 + .. + t_{10}^2}{2} - \text{Correction factor} = 696.16$$

$$\Sigma_3 = a_1^2 . + . b_{10}^2 - \text{Correction factor} = 4{,}034.36$$

$$\Sigma_4 = \Sigma_3 - \Sigma_2 + \Sigma_1 = 478.33$$

	Sum of Squares	d.f.	Mean of Squares	F
Between treatments	2,859.87	1	2,859.87	53.81
Between samples	696.16	9	77.35	1.46
Error	478.33	9	53.15	
Total	4,034.36	19		

APPENDIX 4



Scale - 2.5 inches to one statute mile

APPENDIX 5

THE POSITION OF SOIL SITES 1 - 56

1. Rough Syke; East bank, approximately 100 m. to the S. of gate to House field.

1 - 16 At intervals along the banks of Rough Syke.

17. Netherhearth Syke; West bank, 15 m. S. of Moss Burn.

17 - 27 At intervals along the banks of Netherhearth Syke Note: 22 at source then 27 etc.

28. Moss Burn; South bank, 15m. W. of Netherhearth Syke.

28 - 40 At intervals along the banks of Moss Burn.

41. Moss Burn; East bank at junction with Trout Beck.

42. Moss Burn; East bank, approximately 100 m.S.E.of 41.

43. Moss Burn; Small island just S.of bridge opposite Netherhearth shop.

44. Top of small bluff between House gate and Moss Burn.

45. Terrace between wall of House paddock and Moss Burn.

46. Moss Burn; S.E.bank at junction with Rough Syke.

47 - 50 At intervals between 46 and junction of Moss Burn and Netherhearth Syke.

51. Small hollow just S. of path running between Rough Syke and Netherhearth Syke, approximately 100 m. S. of Moss Burn.

52. Rough Syke; East bank between House paddock and stream.

53. Rough Syke, East bank 3 m. S. of gate to House field.

54. House paddock; 5 m.W.of West door of House.

55. Green Hole; Northern end of Limestone soil.

56. Green Hole; Northern end of peat soil.

APPENDIX 6

THE POSITION OF SEARCH AREAS 1 - 21

1. Moor between Netherhearth Syke and Moss Burn, within 500 m. of Burnt Hill.
2. Burnt Hill.
3. Knock Fell; grassland on Northern edge of top.
4. Burnt Hill.
5. Burnt Hill.
6. House Hill.
7. Hearth Hill.
8. Moor between Rough Syke and Netherhearth Syke, within 500 m. of Burnt Hill.
9. Banks of Netherhearth Syke from junction with Moss Burn for approximately 600 m.

10. - 19. Banks of Netherhearth Syke from source to junction with Moss Burn, divided by position of Soil sites 17 - 27.

20. Hard Hill; sandstone grassland (Off the map in App.4)

21. Burnt Hill.

APPENDIX 7

THE POSITION OF EXPERIMENTAL SITES 1 - 34

1. Rough Syke; West bank 2 - 300m. S. of junction with Moss Burn.
2. Burnt Hill; Southern top.
3. Flats at the Eastern base of Burnt Hill.
4. House Hill; N. of fence dividing House field from moor.
5. House Hill; S. of fence dividing House field from moor.
6. Moor between Netherhearth and Rough Sykes; 3-400m. S. of Moss Burn.
7. Burnt Hill; Southern edge of top.
8. Hearth Hill; Western top.
9. Valley bog; Western edge.
10. Valley bog; Southern edge.
11. Bog Hill; Western slope.
15. Netherhearth Syke; East bank 2-300m. S. of junction with Moss Burn
17. Burnt Hill; Southern edge of top.
18. Terrace between wall of House paddock and Moss Burn.
19. Knock Fell; Northern edge of top.
20. - ditto -
21. - ditto -
22. - ditto -
23. Hollow above point of emergence of Netherhearth Syke at top of slope.
24. 200m. N.E. of 23 on <u>Nardus</u> covered slope.
25. Burnt Hill; Eastern slope.

26. Valley bog; Southern edge.

27. Rough Syke; West bank at junction with Moss Burn.

28. Terrace between wall of House paddock and Moss Burn.

29. Top of small bluff between House gate and Moss Burn.

30. *Juncus* area between Netherhearth shop and the road.

31. Moss Burn; East bank at junction with Trout Beck.

32. Trout Beck; South bank opposite 31.

33. Burnt Hill; S.E. slope.

34. Valley bog; Southern edge.

APPENDIX 8

THE PERCENTAGE LOSS ON IGNITION AND WATER WEIGHT OF ONE SAMPLE OF EACH OF SOIL SITES 1 - 54

Site	Sample Dry weight	Loss on ignition as a % of dry weight	Water weight as a % of dry weight
1	6.989g.	17.31	124.65
2	7.412g.	17.03	81.71
3	8.026g.	15.61	98.39
4	2.804g.	47.82	401.52
5	Lost before examination.		
6	10.285g.	12.27	66.27
7	8.612g.	16.00	90.25
8	7.356g.	22.74	117.5
9	5.579g.	29.27	143.60
10	8.811g.	16.96	86.36
11	5.946g.	30.50	167.50
12	4.444g.	43.38	176.10
13	3.591g.	50.49	222.97
14	4.699g.	35.51	158.90
15	10.671g.	14.15	76.21
16	8.180g.	13.75	87.79
17	10.422g.	14.19	69.60
18	8.542g.	16.44	107.28
19	10.486g.	14.96	94.72
20	4.547g.	33.03	199.80
21	5.693g.	22.61	145.03
22	4.525g.	33.17	173.00
23	4.910g.	31.31	136.29
24	6.618g.	17.04	98.90
25	5.493g.	20.35	187.31
26	2.392g.	75.46	343.89
27	3.297g.	68.55	263.92
28	7.585g.	18.40	93.30
29	8.274g.	11.04	79.80
30	5.335g.	28,92	145.21
31	10.821g.	10.47	37.08
32	8.140g.	12.77	76.50
33	9.170g.	11.99	83.86
34	8.283g.	19.94	90.90
35	7.105g.	16.30	77.27

APPENDIX 8 (Continued)

Site	Sample dry weight	Loss on ignition as a % of dry weight	Water weight as a % of dry weight
36	7.865g.	14.30	71.40
37	5.283g.	26.63	215.80
38	7.582g.	24.42	114.58
39	8.973g.	13.87	57.89
40	6.090g.	23.50	168.81
41	7.368g.	12.86	103.88
42	12.014g.	10.33	67.59
43	6.913g.	26.06	116.80
44	6.929g.	18.17	125.70
45	5.830g.	27.95	154.89
46	8.551g.	16.73	93.52
47	3.234g.	41.06	184.20
48	7.570g.	14.07	97.81
49	8.838g.	12.00	85.11
50	4.480g.	33.42	170.08
51	6.042g.	24.96	148.13
52	4.411g.	29.72	174.00
53	6.138g.	21.28	113.50
54	7.414g.	19.88	108.42

APPENDIX 9

POSITION OF THE SAMPLES IN SOIL SITES 43 AND 54

S.S.43

25	20	3	10	15
24	19	1	9	14
23	18	2	8	13
22	17	4	7	12
21	16	5	6	11

S.S.54

21	20	11	10	4
22	19	12	9	3
23	18	13	8	2
24	17	14	7	1
25	16	15	6	5

APPENDIX 10

SPECIES PER SAMPLE OF 1/25th.sq.m.

S.S.43

No.	L.rub.	L.fes.	D.rub.	O.cya.	A.chl.	A.cal.	E.ros.	E.tet.	Total
1	3			4	11	8	4		30
2	1			2	7	2	1		13
3	13		1		8	2	6		30
4	1		1		11				13
5	1				10	5	3		19
6	2				10	3	5		20
7	1			1	6	2	6		16
8					4	3	5		12
9				4	7	2			13
10	7			2	10		4		23
11	5	1	1		10	1	4		22
12				1	7	2	1		11
13	1			1	7	1	4		14
14	4			2	9	1	4		20
15	1			2	11	1	5		20
16			1		3	3	2		9
17	1			1	5	3	4		14
18		1	2	2	10	3	4		22
19	2		2	2	12		6	1	25
20	2		1	2	10	3			18
21			2		14	3	5		24
22	1				17		2		20
23					12	1	3		16
24				2	12	2	2		18
25	3		3		18	3	1		28
Total	49	2	14	28	241	54	81	1	470

APPENDIX 11

SPECIES PER SAMPLE of 1/25th.sq.m.

S.S.54

No.	L.rub.	L.fes.	D.rub.	O.cya.	A.chl.	A.cal.	A.ter.	E.ros.	Total
1	2	4	1	3	1	1	2		14
2	1	2		4		4	1		12
3	3	3	2	2	1	4	1		17*
4	2	4	2			2	1		11
5	2	4		6		3	2		17
6	2	3	1	3		5	1		15
7	2	2		6		5	2		17
8	3	5		6		4	4		22
9	6	3	2	1		5	4		21
10	5	2	1	2	1		2		13
11	7	2	1	1		1			12
12	6	4	3	2	1	4			20
13	1	2		1		7	2		13
14	1	1		4		5	2		13
15	3	2		2		3	2		12
16	4	2	1	11		6	1		25
17	7	6		5	1	6	3		28
18	3	5	1	2		5	1		17
19	3	2	2			3	1		11
20	3	1	3			1	1		9
21	2	1	1	2		3	1		10
22	5	4		2	1	2	3		17
23	2			7		6			15
24	3		1	8		3	1	1	17
25	1		2	3		5			11
Total	79	64	24	83	6	93	38	1	389

*Includes 1 L.terrestris.

APPENDIX 12

DETAILS OF SEARCH AREA 21

	Eriophorum				Sphagnum				Calluna			
Sample No.	Dung – worms	Dung + worms	Total dung	No. of worms	Dung – worms	Dung + worms	Total dung	No. of worms	Dung – worms	Dung + worms	Total dung	No. of worms
1	4	2	6	2	7	2	9	2	15	3	18	6
2	3		3		5	1	6	1	8	2	10	3
3	5		5		3	3	6	6	7	3	10	3
4	6	1	7	1	6	1	7	2	6	4	10	7
5	4		4		7	8	15	27	4	5	9	8
6	2		2						9	7	16	8
7	1		1		5		5		23	9	32	19
8	2	1	3	1	3	2	5	2	16	6	22	11
9	4		4		2		2		13	7	20	19
10	5		5		6	1	7	1	4	1	5	1
11	4	1	5	1	4		4		11	4	15	8
12	1		1		6	2	8	1	9	2	11	3
13	3	2	5	4	2		2	-	5	5	10	9
14	4	1	5	1	4		4		12	3	15	4
15	4		4			1	1	1	3		3	
16	1		1		3	2	5	2	3	1	4	1
17	7		7		1	1	2		3		3	
18	8		8		2		2		3	2	5	2
19	3		3		9		9		13	2	15	5
20	3		3		7	1	8	1	9	4	13	4
21	7		7		4		4		12	5	17	5
22	3		3		2		2		9	6	15	6
23	5		5		6		6		6		6	
24	3		3		3	2	5	3	4	2	6	2
25	4		4		2		2		9	1	10	1
Total	96	8	104	10	99	27	126	49	216	84	300	135